DECOMPOSITION AND CARBON LOSS IN LODGEPOLE PINE (*PINUS CONTORTA* VAR. *LATIFOLIA*) WOOD FOLLOWING ATTACK BY MOUNTAIN PINE BEETLE (*DENDROCTONUS PONDEROSAE*)

by

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ABSTRACT

Mountain pine beetle (MPB)-killed wood remaining on the landscape is predicted to release significant amounts of carbon to the atmosphere as it decays. A lack of field-based wood decomposition data for validating simulation models reduces certainty in such predictions. Using a chronosequence approach, I quantified decomposition of MPB-killed wood to improve decay rate parameters. Changes in carbon density over time and climatic variability showed distinct patterns for bole position categories. Snag carbon density was similar to that of live lodgepole pine, and did not change considerably with time or climatic influences. Decay in suspended boles increased with summer precipitation, but declined with increasing summer temperature, suggesting decay in elevated boles is moisture-limited on warmer sites. Down boles decayed four times faster with increasing proximity to the soil than suspended boles, but did not clearly reflect climatic influences. Position of dead boles appears more important for wood decay than previously thought.

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INTRODUCTION

Context

Between the 1990s and early 2010s, lodgepole pine (*Pinus contorta* var. *latifolia*) forests in British Columbia (BC) succumbed to a mountain pine beetle (*Dendroctonus ponderosae*) (MPB) attack exceeding the magnitude of any previously documented outbreak[1] (Wilson and Tkacz 1996, Taylor et al. 2006, Wagner et al. 2006). In 2013, the BC provincial government's estimate of the affected outbreak area was 18.3 million ha (MFLNRO 2013), approximately equivalent to one fifth of BC's land base. The extent of MPB-induced tree mortality spurred forest research activities on an array of topics, such as MPB ecology (Carroll and Safranyik 2003), climate change and MPB range expansion (Cudmore et al. 2010), interactions of wildfire and MPB disturbance (Hawkes et al. 2003, Axelson et al. 2009), economic impacts of MPB (Pousette and Hawkins 2006), fall rates of MPB-killed snags (Lewis and Thompson 2009), and shelf life of MPB wood (Woodward 2010), for example. In spite of widespread efforts to salvage MPB-killed trees and minimize wood quality losses, much of this wood will remain on the landscape to degrade by natural processes (e.g., fungal decomposition, fire) (Pedersen 2003, Wagner et al. 2006, Cornwell et al. 2009).

Broadly speaking, forests are considered a major sink for atmospheric carbon dioxide (CO_2) at the global scale because of their capacity to sequester carbon via photosynthesis into long-lived

[1]Based on a maximum observation period of approximately 160 years, this is the most extensive MPB outbreak on record. Field and aerial surveys for MPB attacks date back to the early 1900s in BC; dendrochronological cross-dating records extend back no further than the 1870s in BC (Heath and Alfaro 1990, Taylor et al., 2006), and the early 1800s in the US (Thorne 1935, Cole and Amman 1980, Mitchell et al. 1983, Wilson and Tkacz 1996). No evidence of documented First Nations' knowledge of MPB outbreak history was found.

wood biomass. As such, living forests play a major role in regulating climate conditions by offsetting the "greenhouse" effects resulting from rising atmospheric CO_2 (Grace 2005, IPCC 2007). The capacity of forests to fulfil this buffering role, however, is responsive to climate. Due to rising concentrations of anthropogenic CO_2 and other greenhouse gases [GHGs] in the troposphere, more solar energy is being trapped and reradiated back to Earth, contributing to warmer surface temperatures (IPCC 2013). Under warmer surface conditions, many forest disturbance agents including insect outbreaks and fire may occur with greater frequency, severity, and/or distribution (Carroll et al. 2006, Haughian et al. 2012). Forest disturbances result in a greater abundance of dead organic matter on the landscape, and a subsequent release of CO_2 as this material decays. Therefore, forests may actually exacerbate global GHG emissions by succumbing to large-scale disturbances, resulting in a surplus of decomposing wood (Volney and Fleming 2000). In this context, large MPB outbreaks have the potential to surpass local, regional, and even provincial scale impacts by rendering Canada's forests a net carbon source, rather than a sink (Kurz et al. 2008, Hicke et al. 2012).

This thesis focuses on the loss of carbon from dead lodgepole pine wood following MPB attack, with the goal of improving the understanding of decay rates and therefore, implications for atmospheric CO_2 contributions from forest disturbances. In the following background section I review leading methodologies for estimating forest carbon fluxes and wood decay, with emphasis on the approach used by Canadian Forest Service researchers for forest carbon accounting. I then briefly review a few of the leading factors affecting wood decomposition in natural landscapes. In the methods section I describe the field, laboratory, and statistical procedures used for all phases of the project. These include the methods for a precursory assessment of wood density as a surrogate for carbon density, as well as the main investigation

of carbon loss from decaying MPB-killed lodgepole pine wood. My findings for the preliminary work and focal research are presented in the results section. In the discussion, I talk about the results and implications of the project in the context of existing literature, with special attention on how this research applies to the Canadian Forest Service's national forest carbon budget model. I also share some reflections about forest ecosystem integrity, and thoughts for future research. In the conclusions I highlight the main points of the research.

Background

Metrics of forest carbon fluxes

Various approaches have been employed in efforts to quantify ecosystem-level forest carbon fluxes under both undisturbed and disturbed conditions. Regardless of the methodology or ecosystem state, carbon flux quantification involves certain basic metrics which are either measured directly or inferred over seasonal or annual time periods. These include 1) the total amount of ecosystem photosynthesis (gross primary productivity – GPP), 2) carbon released by vegetation during respiration (autotrophic respiration – R_a), 3) net carbon sequestered by vegetation (net primary productivity – NPP, defined as GPP - R_a), 4) the amount of carbon lost through decomposition or herbivory (heterotrophic respiration – R_h), and 5) the net carbon sequestered by an ecosystem (net ecosystem productivity – NEP, defined as NPP - R_h) (Chapin et al. 2006, Hicke et al. 2012). These terms are generally expressed in units of g C m^{-2} yr^{-1}, requiring specification of both an area and a time period with the affiliated carbon quantity. Positive NEP values indicate that a system has accumulated carbon (i.e., was a net sink), whereas

negative NEP values indicate that a system has released more carbon than was sequestered (i.e., was a net source) over a given period[2].

Disturbances such as MPB interrupt the net carbon storage capacity of forests in two ways. First, photosynthetic carbon sequestration (GPP) is arrested, which occurs immediately when trees die. The second is a much slower response: the volume of dead wood going through the process of decomposition (R_h) increases relative to live biomass and pre-outbreak levels of dead organic matter (DOM), thereby amplifying the amount of carbon being released back to the atmosphere. This long-term gradual response of coarse woody debris (CWD) represents the fate of the majority of carbon stored in above-ground biomass in conifer forests (Bois et al. 2009).

Approaches for quantifying forest ecosystem carbon fluxes

Measuring biosphere exchanges of gases (e.g., CO_2) has an established history in the fields of plant physiology and ecology (Heinicke and Childers 1937, Thomas and Hill 1937). Early work involved closed-chamber gas exchange rate measurements which were only capable of capturing at the scale of single leaf, plant, or small soil units over short observation periods (Heinicke and Childers 1937, Musgrave and Moss 1961, Schulze and Koch 1971, Field et al. 1982). Many biases and assumptions limited the extent to which these observations could be interpreted, making ecosystem-scale extrapolations fundamentally problematic (Rochette et al. 1992, Lund et al. 1999).

Quantifying carbon stocks and stock changes later became an independent way to measure ecosystem carbon fluxes, as well as a means to verify extrapolated flux estimates from fine-

[2] Similar to NEP, net ecosystem exchange (NEE) is the net flux expressed relative to the atmosphere, rather than the ecosystem. Therefore, the sign is reversed: positive NEE indicates a net increase in atmospheric carbon, negative NEE implies a net loss of atmospheric carbon and gain to the ecosystem (Hicke et al. 2012).

scaled gas exchange measurements. Carbon stocks are quantified by assessing soil carbon concentration, soil organic layer thickness or volume, living biomass volume, and annual inputs of litter and CWD, for example. Jenny's (1950) work established this approach by making the assumption that, for stable forest ecosystems, "...the annual rate of addition of organic carbon is equal to the annual rate of loss," (NEP = 0). The extension of Jenny's assumption is that for systems not in equilibrium, the changes in carbon stocks represent the net ecosystem carbon flux (NEP $\neq$ 0). Measuring carbon stocks has persisted as an important tool not only for verifying gas exchange measurements, but for estimating landscape-scale carbon fluxes directly (Laiho and Prescott 1999, Matsuzaki 2011).

Subsequent improvements in closed-cell gas exchange technology, together with advances in micrometeorological instrumentation (Baldocchi 2003), enabled the evolution of open-chambered gas sensors (Bowen ratio / energy balance system) (Spittlehouse and Black 1980, Held et al. 1990), and three-dimensional open-air sensors (eddy-covariance technique) (Swinbank 1951, Mooney 1972, Wesely et al. 1983). This technology bypassed the spatial and temporal limitations of the closed-cell systems. Eddy covariance instruments measure CO_2, H_2O, and energy fluxes from ecosystems, permitting the estimation of forest-scale carbon flux variables such as R_h and NEP (Baldocchi et al. 1988). As part of the 'Fluxnet Global Network' (2013), eddy covariance systems are now stationed at several hundred sites worldwide, and are recognized as integral tools for stand and landscape-scale estimates of ecosystem gas exchange (Baldocchi 2003).

With the growing importance of understanding global-scale carbon fluxes as a driver of climate change, other methods have emerged for performing CO_2-flux measurements over even larger

areas. Remote sensing has been shown to effectively infer variables such as atmospheric CO_2 concentrations, biomass per unit area, land cover/use and – given adequate record sequences – land cover/use changes (Grace 2005), and gross primary productivity (Running et al. 2004). Atmospheric inversion models use a hybrid of remotely-sensed atmospheric CO_2 concentration data, land surface information, and computer simulation modelling to extrapolate CO_2 fluxes over a very broad scale (Dolman et al. 2005). Light Detection and Ranging (LiDAR) has also been reported effective for assessing three-dimensional canopy structure for upscaling eddy covariance measurements of gross ecosystem productivity to landscape scales (Hilker et al. 2008a). Integration of multiple data sources and comparison of ecosystem carbon flux estimates among independent methodologies has yielded validation and support for these technologies.

Computer-based simulation models represent a well-developed approach for estimating ecosystem carbon flux parameters such as NEP. Models generally contain three categories of components: 1) pools (stocks) which accumulate and store carbon, 2) transfer mechanisms that move carbon between pools, and 3) factors that regulate transfer rates and therefore, the size of the pools (Chen et al. 2000a). A major distinguishing factor among models is the methodological approach used to simulate sequestration of carbon in the modelling framework. There are two primary categories of models. In *process-based* models, carbon sequestration is computed from empirically derived relationships between physiological parameters such as photosynthesis, and environmental factors such as atmospheric and growing condition variables (Waring et al. 2014). By responding to external control factors, process-based models inform how changes in environmental conditions may mechanistically influence changes in forest carbon stocks and fluxes. In contrast, *inventory-based* models simulate carbon sequestration as a function of growth and yield relationships, which are derived from historic growth data for

specific forest age classes and stand types (Kurz et al. 2009). This distinction makes inventory-based models suited to predicting how forest growth and carbon balances may be affected by management practices and natural disturbances (Kurz et al. 2009) under static environmental conditions.

Canada's carbon budget model and carbon flux predictions for MPB disturbance

Of the numerous methodologies that exist for quantifying forest carbon fluxes, inventory-based computer simulation modelling is the approach used by Canadian Federal researchers for national-level carbon accounting and reporting. The Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3, or CBM) was initiated in the early 1990s in accordance with the Intergovernmental Panel on Climate Change (IPCC) standards and the Kyoto Protocol mandate (Kurz et al. 1992, Kurz and Apps 2006) to assess the impacts of disturbance, climate change[3], and forest policy options (Kurz et al. 1992) on the carbon balance of managed Canadian forests. The CBM-CFS3 is therefore parameterized specifically to estimate national-scale forest carbon stocks and fluxes in Canada, and it is the primary source of information used by the Canadian government for national-level carbon accounting.

Like other carbon flux simulation models, the CBM-CFS3 is based on a structure incorporating carbon pools, carbon transferring processes, and transfer regulating mechanisms. As of 2009, the model included 21 carbon pools, and numerous sub-models to represent above- and below-ground annual tree growth, litter fall, biomass turnover and decay. The model incorporates

[3] Although assessing impacts of climate change was specified as one of the mandates for the CBM-CFS, an inventory-based modelling approach does not have the capacity to respond to climate change factors (Kurz, pers. comm.).

explicit detail for the disturbance processes of harvesting, mortality from insect and fire and associated forest fuel consumption (Kurz et al. 2008).

In 2008, the Canadian carbon modelling team published results applying the CBM-CFS3 specifically to the MPB disturbance in BC. Based on model output, Kurz et al. (2008) predicted that BC's MPB-killed stands would release an average of 36 g C m^{-2} yr^{-1} between 2000 and 2020 due to the surplus of decaying wood, accelerated harvesting, and forest fires on MPB-affected landscapes. Although this prediction may be plausible, external validation of CWD decay rates is an outstanding need (W. Kurz, personal communication, 2014), and the sign, magnitude and timing of net carbon emissions following MPB attack – specifically decay-related carbon emissions – remain topics of debate. Eddy covariance (fixed and roving tower) measurements made since 2007 in several locations within the MPB-affected area in central BC show that recovery of NEP following beetle attack has occurred rapidly (Brown et al. 2010; 2012). The observed increase in NEP was due to an increase in GPP. Furthermore, NEP and foliar gas-exchange measurements indicated a significant increase in photosynthetic capacity, largely because of understory tree recovery (Bowler et al. 2012). Evidence of a significant increase in R_h has not emerged from the eddy covariance measurements, indicating that decomposition of the additional dead organic matter is slow, contrary to the CBM-CFS3 predictions (Brown et al. 2010; 2012).

Limitation of decomposition (R_h) estimates in the CBM-CFS3

Scientific models gain internal validation (reliability) when their limitations are clearly delineated through a process of sensitivity, uncertainty, and error analyses. Model estimates garner broader acceptance when external validation occurs through comparison with results from

empirical and independent methods. Many components of the CBM-CFS3 have been extensively calibrated, tested and verified (White et al, 2008, Smyth et al. 2010, Shaw et al. 2014), and have established credibility with the Canadian federal government and the IPCC community (Environment Canada 2011). However, despite the model's wide usage in Canada, one of its most important components – the decomposition rates for dead trees – lacks adequate substantiation by field-based observations, particularly in the context of tree mortality associated with the recent MPB epidemic in BC.

Original decomposition rates used in the CBM were based on personally-communicated estimates by M. Harmon and A. Trofymow, who independently have extensive experience studying litter turnover processes in forests. Harmon and Trofymow developed decay rate estimates for the *Moderate Temperate* ecoclimatic province of southern Ontario[4] (Kurz et al. 1992). These original estimates then served as reference decay rates for all DOM pools[5] in the CBM. Regionally-specific decay rates for the other ten Canadian ecoclimatic provinces and their respective DOM carbon pools were derived as a function of the reference decay rates and local mean annual temperatures (Kurz et al. 1992).

In 2009 and 2010 the CBM team calibrated the DOM sub-model with data from the Canadian Intersite Decomposition Experiment (CIDET) – a project designed to evaluate litter decay over a 12-year period at 16 forested sites across Canada (Trofymow et al. 2002, Smyth et al. 2010). These improvements included adjusting decay rates and expanding other decay parameters to

[4] Harmon and Trofymow have extensive knowledge of decomposition processes in ecosystems of the Pacific Northwest and BC's west coast, respectively. Harmon has also studied wood decomposition in northwestern Russia. However, I was unable to find studies by either scientist in ecosystems of southern Ontario, for which the reference decay rates were developed, and upon which all other CBM decay rates were subsequently based.

[5] See Table A1 in Appendix A for descriptions of the CBM-CFS3 DOM pools.

more accurately represent DOM carbon pools and processes. Even though the CIDET project verified CBM decay rates, it only assessed litter material classified in the very fast and fast pools (litter, fine woody debris (FWD), roots, and stumps). To date, the medium decay rate – which represents decomposition of merchantable-sized stem wood (i.e., CWD and snags) and the largest above ground carbon pool – has had little verification due to a shortage of suitable field-based data at appropriate spatial scales for national-level modelling (W. Kurz personal communication, 2014).

Kurz et al. (1992) and others (Yin 1999, Zhou et al. 2007, Smyth et al. 2010) have stated this knowledge gap exists regarding decomposition rates, largely because of the challenges and limitations of quantifying the heterogeneous processes of wood decay (Lambert et al. 1980, Graham and Cromack 1982). In spite of the challenges, however, the topic has been addressed in a number of comprehensive textbooks (Scheffer 1973, Rayner and Boddy 1988, Zabel and Morrell 1992), journal articles (Rayner and Todd 1979, Harmon et al. 1986, Yin 1999, Cornelissen et al. 2012, Jomura et al. 2008, Shorohova and Kapitsa 2014), and technical reports (Bull 1983, Maser and Trappe 1984, Lewis et al. 2006) over recent decades. I will review this literature in the following section, with emphasis on lodgepole pine when possible.

Methodologies for quantifying wood decay

Early efforts to quantify decomposition rates resulted in what was known as the equilibrium principle (Jenny 1950). In other words, if climatic and environmental conditions are stable, accumulation of dead biomass material in a forest will eventually reach a point when the rate of decomposition matches the rate of input, thereby resulting in a relatively constant volume of organic material on the forest floor. With this assumption, the rate of decomposition could be

evaluated by measuring the annual input of litter material. This conceptual model for estimating decomposition rates has been used by many (Olson 1963, Minderman 1968), and is frequently cited in recent decomposition studies (Johnson and Greene 1991).

Real-time methods for quantifying wood decay include closed-cell chambers either attached to or completely enclosing CWD. Instantaneous rates of CO_2 evolution are measured as the air within the chamber is circulated through a gas analyzer system. Similar to Boddy's (1983a) enclosed chamber for branch respiration measurements, Jomura et al. (2008) developed a large-volume chamber for measuring instantaneous CO_2 release from decomposing logs at forested field sites in Japan. Closed-cell chamber methods have been used both independently and in conjunction with other methodologies as a means of verifying components of whole-ecosystem CO_2 fluxes (Emmel et al. 2014).

Like real-time chamber measurements, long-term monitoring approaches also use real-time observations, but mass or volume losses due to decomposition are determined by re-measuring sample specimens that have been exposed to field conditions over specific periods of time (e.g., years or decades), rather than measuring instantaneous rates. The moisture-corrected difference between consecutive measurements signifies the loss of mass or volume over time. Two country-wide long-term litter decomposition studies have been conducted in North America: one over a 10-year period in the US (LIDET 1995, Gholz et al. 2000), and another over a 12-year period in Canada (CIDET, Trofymow et al. 2002). These studies have yielded some of the most spatially broad datasets for litter decomposition. More so than for litter, long-term studies evaluating wood decay pose a greater challenge because of the inherently slow nature of the process. In spite of the logistical challenges, however, several longer-term monitoring

experiments have successfully executed wood decay rate estimates over, for example, 20 years (Herrmann and Prescott 2008), and even 65 years (Stone et al. 1998).

The more common method for estimating decay rates is the chronosequence approach, which has been used in numerous studies in recent decades (e.g., Graham and Cromack 1982, Means et al. 1985, Johnson and Greene 1991, Busse 1994, Brown et al. 1998, Beets et al. 2008, Ryan et al. 2008, Angers et al. 2010). Also known as a retrospective approach, chronosequence studies rely on dendrochronological analysis (tree ring dating) to determine the year of death and/or fall of woody debris (Means et al. 1985). Losses of mass or density are calculated based on an assumed maximum at the time of tree death (Busse 1994). The decay rate is determined by dividing the change in wood mass or density by the number of years since tree death (e.g., g cm^{-3} yr^{-1}). Although there are more potential sources of error associated with the chronosequence method (Means et al. 1985), it is frequently employed because of the logistically simpler data collection process that requires only a single visit to field sites while still enabling multi-year or multi-decadal observations (Walker et al. 2010).

In 2000, M. Harmon and colleagues introduced the decomposition-vector method for evaluating wood decay in a simultaneous comparison with the chronosequence approach. The vector method hybridizes chronosequence and long-term monitoring methods; it relies on dendrochronological dating to establish years-since-death, combined with short-term re-sampling – in this case 3 years – to capture a specific period (i.e., 3 years) of the decay process following tree death. In this way, the short-term decay rate (over the 3-year period) can be compared with the overall decay rate from the time of tree death to ascertain changes in the decay rate over over time (Harmon et al. 2000).

Factors affecting wood decay

Decomposition of wood is influenced by an array of environmental variables that interact within and across spatial and temporal scales (Lambert et al. 1980, Harmon et al. 1986). This complexity has been described by Laiho and Prescott (2004) simply as derivatives of two key factors: substrate quality and environment. However, the intricate network of confounding "derivative" influences is extensive, and untangling them remains an important yet daunting proposition for researchers (Maser and Trappe 1984, Yin 1999). Given these layers of complexity, the factors affecting wood density described here are not intended to be comprehensive, but rather a brief highlighting of some of the leading factors and corresponding relationships that have been identified in the literature.

Temporal

Among the many complex influences challenging the quantification of decay rates is time itself (Graham and Cromack 1982; Maser and Trappe 1984, Yin 1999). The sheer time required for decomposition to progress dwarfs typical short-term study designs by exceeding convenient observation periods (Harmon et al. 1986, Johnson and Greene 1991). Beyond this technical challenge, the time for complete decomposition extends well beyond human lifespans, which inherently limits our capacity to comprehend the suite of processes occurring from the time a tree dies to when it is entirely assimilated into other forms.

Another aspect of the temporal dimension of wood decay concerns the variability of CWD inputs over time. Forests with mixed age-class structures and small-scale/single-tree mortality events are likely to have an even distribution of dead wood across all decay classes at all times (Graham

and Cromack 1982). In contrast, landscapes having even-aged forests are more likely to undergo phases of low and high CWD inputs as stands uniformly mature and succumb to disturbances (Sturtevant et al. 1997, Page and Jenkins 2007). Thus, even-aged stands may have an entire forest cohort proceeding through decay classes at approximately the same time. Whole-ecosystem decay rates for these two scenarios would therefore be very different: the first having a relatively stable rate of decay, the second having periods of high and low decay rates.

At the individual tree level, the onset of decomposition following tree death can be rapid or extremely slow, dictated largely by bole-specific conditions of resource quality and microclimate suitability (Harmon et al 1986, Rayner and Boddy 1988, Yin 1999, Laiho and Prescott 2004). These micro-scale conditions ultimately determine the onset and rate of wood decay, but are, in turn, controlled by factors that act at coarser spatial scales, which will be considered next.

Climate

Optimal conditions for microbial decomposition occur when wood remains moist at moderate temperatures. Toward the limits of optimal temperature and moisture ranges, microbial processes decline, and at extremes of hot or cold, dry or wet, decay activity can be inhibited entirely (Zabel and Morrell 1992). Climate therefore, by regulating temperature and moisture inputs, plays a major regulatory role in wood decomposition.

At the microclimate scale, most decay fungi thrive between 20 and 30 °C (Deverall 1965, Scheffer 1973, Rayner and Todd 1979, Boddy 1983b), although Zabel and Morell (1992) reported optimal temperatures ranging from 15-45 °C. For some decay fungi, survival thresholds can be below 0 °C, or as high as 60 °C (Deverall 1965). Chen et al. (2000b) found that CO_2

release from decomposing lodgepole pine roots peaked at 30 °C, which was about ten degrees lower than the peak respiration temperature for dead roots of other conifers in the same region of Oregon.

Many decay fungi require a minimum wood moisture content around 30 % of dry wood weight, (Käärik 1974, Rayner and Todd 1979) and exhibit peak growth within a range of 40-80 % moisture (Scheffer 1973, Rayner and Todd 1979). This range varies, however; Käärik (1974) reported growth of decay fungi in moisture conditions up to 160 %, and Boddy (1983a) showed peak CO_2 release from decomposing branches having moisture contents of nearly 200 %. Peak respiration rates for dead woody lodgepole pine roots were reported between 125 and 225 % moisture by Chen et al. (2000b).

Boddy's work (1983a) illustrated the interdependence of temperature and moisture and their combined effects on decomposition rates. When temperature was held steady at 15 °C with increasing moisture, CO_2 release from decaying branches increased to a maximum then declined. A similar pattern was observed at 25 °C, but with a much greater CO_2 release, suggesting that at higher temperatures and higher moisture contents, the maximum respiration rate also increases. Respiration rates of pine CWD in a temperate broad-leaved forest in Japan exhibited an exponential response to temperature, and a quadratic response to moisture (Jomura et al. 2008). The decline of respiration at higher moisture contents observed by Boddy (1983a) was attributed to constricted gas exchange as voids in the substrate became filled with water. The internal microclimate of wood can therefore affect gas exchange potential (Boddy 1983a), fungal growth rates, and fungal species assemblages (Boddy 1983b, Son et al. 2011) which I discuss in more

detail later on. Thus, temperature and moisture affect wood decay rates *indirectly*, as well as directly.

If one imagines zooming out from the micro-scale to a broader perspective, microclimate conditions themselves are dictated by many factors, such as host tree species (Alban and Pastor 1993) and wood density (Boddy 1983a), and at an even broader scale, by regional climate (Jenny et al. 1949). Yin's (1999) integrative approach for estimating decay of woody debris in field conditions led to the conclusion that, in addition to tree species, latitude and elevation, January and July temperatures and precipitation were key parameters defining decay rates. Accordingly, latitude and seasonality influence wood decay rates by determining the form of precipitation (e.g., snow versus rain), annual temperature cycles or lack thereof (Jenny 1950), and hence, the extent of exposure to ideal decay conditions. Coastal and tropical regions where precipitation falls as rain year-round have a greater potential for rapid decay, compared to areas that have sub-zero winter temperatures and/or hot dry summers (Jenny et al. 1949). At higher latitudes, depth and duration of snow cover can influence the rate of decay for wood at or below the snow surface; though growth of mesophilic[6] fungi may be supressed, other cold-tolerant fungal species can remain active in the cold moist conditions under the shelter of snow (Käärik 1974).

Over time, the collective effects of physical, chemical, and biological processes (which I will discuss in more detail below) render wood tissue more prone to mechanical weathering. Hence, repeated wetting and drying, freezing and thawing events (Zhou et al. 2007) that are relatively negligible factors in the early stages of wood decay may be more significant players later on, following initial chemical breakdown by microbes.

[6] Mesophilic: thriving at moderate temperatures.

Physical

The physical size, position, and extent of fragmentation of CWD are other factors affecting the microclimate and substrate conditions that dictate decay potential. Compared to smaller pieces of CWD, large logs have low surface-area-to-volume ratios, which can limit the penetration of decay agents from external sources (Harmon et al. 1986). Therefore, the rate at which dead wood becomes colonized and degraded by decay organisms may to some extent depend on bole size, although efforts to demonstrate this size dependency have yielded inconclusive results (Harmon et al. 1986).

Other size-related issues include the dependence of volume on moisture content. The diameter of wood samples is often used to determine sample volume and density, which can then be used to indicate the extent of decomposition. However, the moisture content of wood affects the volume; disproportionate shrinkage in wood occurs when the internal humidity drops below the fibre saturation point (30 %) (Barton and Brownell 1981, Harmon et al. 1986), resulting not only in loss of volume, but also in checking (cracking) (Lewis et al. 2006).

If dead trees remain standing, they may persist as snags without substantial decay (Johnson and Greene 1991) for considerable lengths of time. Trees with pre-existing root rot or butt rot at the time of death are more likely to fall sooner and follow an accelerated path of degradation (Angers et al. 2010). If otherwise uninfected, snags may persist standing for many years to decades because they are less accessible to soil-borne decomposers, intercept less precipitation by being vertical, and retain less moisture, e.g., because of gravitational flow down the stem and exposure to canopy air movement and evaporation (Bull 1983, Fahey 1983). By remaining in an upright position snags ultimately avoid exposure to many decay agents (Shorohova and Kapitsa

2014); however, they are more prone to checking (longitudinal cracking) than fallen boles (Lewis et al. 2006). Checking happens more readily in snags because of the drier atmosphere coupled with exposure to temperature extremes. Checking effectively increases bole surface area, and provides a direct pathway for airborne fungal spores to become established internally.

Fallen logs are more readily accessible to agents of decay once they are in contact with the ground (Harmon et al. 1986, Busse 1994); they retain more moisture from precipitation and upward wicking, as well as by being within the relatively protected and humid boundary layer of vegetation and snow cover. The process of falling itself can accelerate the rate of decay when stem breakage occurs (Angers et al. 2010). Snags with pre-existing rot (e.g., from roots, wounds, insect damage, checking, etc.) are more likely to fracture or shatter upon impact (Lewis and Hartley 2006), thus increasing the surface area exposed to moisture and decomposers. Fragmentation, by falling or other causes (e.g., lightning, checking, woodpeckers, mammal excavation, etc.), exposes interior surfaces that would otherwise take much longer for decay pathogens to penetrate.

Chemical

The chemical composition of wood adds another layer of complexity to the challenge of quantifying decomposition. Trees are a heterogeneous combination of chemical compounds that range from volatile, to soluble in certain media, to relatively inert – properties that change over the course of degradation. All trees manufacture cellulose, hemicellulose, and lignin: organic compounds that make up the cell walls of woody tissue. This trio is responsible for the structural support in stem wood and accounts for nearly 100 % of wood mass (Barton and Brownell 1981). The relative amounts of these compounds in lodgepole pine are similar to other softwood tree

species; cellulose is most abundant with lesser amounts of hemicellulose and lignin (43, 32, and 25 % respectively, approximate averages) (Lieu et al. 1979, Kim et al. 1989, Koch 1996). Carbon is the backbone of all three structural compounds, which explains why wood contains approximately 50 % carbon by mass. Other elemental constituents of cellulose, hemicellulose, and lignin vary, as do their molecular size, shape, and structural complexity (Barton and Brownell 1981). These differences result in differential susceptibility to break-down by microbial enzymes. Not only are cellulose and hemicellulose more abundant in wood relative to lignin, they are also the preferred nutrient source for many decay fungi (Harmon et al. 1986).

Other compounds occurring in wood are referred to as extractives and have lower molecular weights than cellulose, hemicellulose, and lignin. Extractives account for less than 4 % of wood mass in lodgepole pine (Kim et al. 1989), and include a range of organic and inorganic compounds (Koch 1996) including resins that are toxic to decay fungi and insects (Barton and Brownell 1981). Extractives can be volatile, water-soluble, or relatively inert (i.e. remain as ash after combustion) (Koch 1996). Though they occur in micro amounts compared to the three cell wall components, extractives largely define species-specific wood traits, including the susceptibility to decay (Barton and Brownell 1981, Harmon et al. 1986, Cornwell et al. 2008). Extractives are therefore key to the tree's defense system against pathogens. The abundance and distribution of extractives in wood are much less predictable than the three major compounds, adding to the complexity of determining specific decay rates.

Biological

A multitude of biological factors influence wood decomposition, from microbial and invertebrate communities, to species-specific wood traits and complex forest stand attributes. Fungi are the primary microbial agents that decompose wood (Scheffer 1973, Käärik 1974, Dolenko et al. 1981) in terrestrial environments (Harmon et al. 1986). Decay fungi specialize in breaking down the compounds of cell walls, degrading the structural integrity of dead wood and causing unique fragmentation patterns. The two main fungal groups responsible for wood decay are brown and white rot fungi (Kirk and Highley 1973). White rot fungi produce enzymes that metabolize both lignin and cellulose, whereas brown rot fungi are only capable of breaking down cellulose (Harmon et al. 1986). Other fungi such as the sap-staining symbiotic partners of the MPB infest and occupy fresh wood, but do not affect cell wall components the way decay fungi do. Rather, they extract nutrients from cell contents without affecting the structural integrity of the wood (Rayner and Boddy 1988). Though they do not break down cell walls directly, sap-stain fungi can facilitate the entrance of decay fungi into the sapwood, predisposing the tree to early onset of decay processes (Lewis et al. 2006).

External environmental factors can influence the diversity and abundance of fungal communities. Higher year-round precipitation in the Prince George region compared to other drier regions of BC was associated with greater diversity of decay fungi (Son et al. 2011). Succession of complementary fungal communities can accelerate decomposition, but if multiple competitive fungal species co-occur, their demand for the same resources can slow the process (Hattenschwiler et al. 2005).

The role of insects in wood decomposition can be considerable, but is much less predictable than that of decay fungi. Primary bark beetles such as the mountain pine beetle may be initially instrumental in excavating the cambium and inoculating sapwood with blue stain fungi, causing tree death (Carroll and Safranyik 2003), and secondary bark beetles may opportunistically follow, mining the cambium while it is relatively fresh. But with or without the influence of primary and secondary bark beetle attacks, dead wood can remain unaffected by wood-boring insects indefinitely (Harmon et al. 1986). If present, however, local populations of termites, carpenter ants, or other insect decomposers (i.e., saproxylic insects) that excavate dead wood can dramatically accelerate its breakdown (Maser and Trappe 1984).

As described earlier, species-specific traits of dead wood such as the chemical constitution and wood density can influence the predisposition of wood to decay (Cornwell et al. 2008, Weedon et al. 2009). But in addition to these factors, overall forest stand characteristics in conjunction with the relative abundance of a host tree's component parts will influence the volume of dead wood available to decomposers at any given time, and therefore, the overall rate of decomposition for the ecosystem. Stand attributes such as age, density, canopy closure, slope, aspect, and elevation affect the volume of dead wood and the microclimate conditions determining decay rates of DOM (Maser and Trappe 1984). Needles, twigs, fine roots, and bark degrade much more quickly than bole wood (Trofymow et al. 2002) because of higher surface area to volume ratios and lower lignin and cellulose contents, but these constituents make up a smaller portion of the tree's biomass, and therefore, a smaller source pool of degradable material. For lodgepole pine in BC, Comeau and Kimmins (1989) reported that the bole constitutes about 70 % of total tree biomass, foliage and branches account for 6 %, and belowground about 24 %. Other studies conducted in western Canada (Johnstone 1970) and northwest US (Little and

Shainsky 1992, Litton et al. 2003) report similar biomass allometry for lodgepole pine. Hence, in addition to the physical and chemical properties of wood described earlier, the relative abundance of tree parts and the total abundance of woody debris on the landscape will influence the overall rate of decomposition for the stand, and ultimately the CO_2 respired to the atmosphere.

Research objective

In an effort to alleviate some of the uncertainty about wood decomposition, the objective of this research was to estimate wood decomposition rates for the case of recent MPB outbreaks in BC. Specifically, my goal was to quantify the carbon released from MPB-killed lodgepole pine wood over the first 40-50 years after tree death, and to characterize the influence of selected environmental attributes on the rate of carbon loss.

Scope of research

Because of the extreme heterogeneity of environmental conditions that influence rates of wood decay, I restricted my research to lodgepole pine boles killed by MPB in the central interior of British Columbia. Limiting the scope of research in this way was valuable for several reasons. First, boles make up the majority of biomass in a tree (Comeau and Kimmins 1989), and therefore, account for the bulk of above-ground carbon storage in forest ecosystems. Second, as dead bole wood is also the carbon pool least characterized in the CBM-CFS3, it was of particular value to focus on this component of forest carbon. And third, trees that have succumbed to the same mode of mortality are more likely to follow similar decomposition trajectories (e.g., MPB galleries and blue stain fungi act as initial pathways for other decay organisms (Lewis et al.

2006). Therefore, focussing my research efforts on MPB-killed boles was a way to eliminate some of the potential noise that could be introduced by including trees that died by other means.

Research question, hypotheses, and methodological rationale

This research set out to answer the question: What are the rates of wood decay as related to a) time since tree death and fall, b) climatic moisture and temperature regimes, and c) bole position (standing, fallen but suspended, or fallen and down on the ground)?

With the support of my committee, I defined the following hypotheses regarding the influences of the parameters of interest. I hypothesized that:

H1: The rate of decay is low to negligible for snags.

H2: Suspended CWD is distinctly different from snags because of the higher catch surface upon which precipitation lands and potentially remains – especially in the case of snow.

H3: Down CWD differs from suspended CWD because, by being in direct contact with the ground, down CWD is more susceptible to colonization by soil-borne agents of decay, as well as up-wicking of soil moisture. Down CWD is also within the boundary layer of ground surface conditions such as vegetation cover in summer, and snow cover in winter.

H4: With respect to climate factors, wood decay rates are faster on sites with higher climate moisture and temperature because of more optimal micro-conditions for biological activity. Likewise, I expected sites with drier and colder climatic conditions to have slower decomposition.

To address the research question, I estimated long-term density loss in dead wood specimens at various stages of decay. I collected samples from MPB-killed boles on sites reflecting a gradient of climatic variability (i.e., moisture and temperature), and assessed the wood density of snags, suspended, and down logs. Year of death and year of fall (for fallen boles) were evaluated using dendrochronological methods. In order to expedite lab work and reduce sample processing costs, I conducted a preliminary assessment of a subset of samples to validate the use of wood density as a surrogate for carbon density. This step allowed me to use simpler laboratory techniques to extrapolate carbon density for the remainder of the sample inventory.

Significance of research

This research is important for several reasons. It will: a) enable better understanding of ecosystem carbon fluxes by delineating one key CO_2 source, which may influence other forest carbon-flux components; and b) provide regionally specific field data upon which to base parameters for the modelling of a major CO_2 source over time. As indicated by Canada's carbon accounting team, the disturbance matrix component of the CBM-CFS3 could be improved if more detailed wood decomposition data were available (W. Kurz and C. Smyth personal communication 2014, 2015). The dataset generated by this research therefore provides a verification tool for the decay rates used by the CBM-CFS3 to estimate Canada's forest carbon fluxes following high-mortality forest disturbance events. Considering the potential impact of the CBM-CFS3 for managing carbon emissions from local to international scales, improving Canada's ability to predict forest-based CO_2 contributions to the atmosphere is a high priority (Johnston et al. 2010).

In addition to direct linkages to the CBM-CFS3, this research has significance for local forest managers in government, industry, and First Nations groups. Given the relevance of carbon-related issues to global climate change, local salvage harvesting following major forest disturbance events will play an important role in the carbon balance of forested ecosystems. Knowledge of forest carbon dynamics can contribute to responsible forest management decisions for long-term viability of ecosystems and a timber harvesting industry. I therefore want to ensure that these findings reach decision makers at the local level.

METHODS

Study area

The study area was located in the sub-boreal central interior of British Columbia between 53.32° and 53.98° N latitude, and 122.41° and 125.11° W longitude (Figure 1). Elevations ranged from 698 to 1252 m ASL. Based on climate normals (1960-1990), mean annual precipitation (MAP) ranged from 300 to 730 mm, and mean annual temperature (MAT) from 1.0 to 3.2 °C (Climate WNA; Wang et al. 2012) (Table 1). Stands selected for sampling were either pure lodgepole pine or pine-leading mixed conifer forests, all with extensive pine mortality due to MPB attack.

Within this region, sites were chosen to reflect a range of climatic moisture in the Sub-Boreal Spruce and Sub-Boreal Pine – Spruce biogeoclimatic zones (Meidinger et al. 1991). By sampling across this climatic gradient, I hoped to capture the range of variability in wood decay that may result from different climate conditions. Based on Biogeoclimatic Ecosystem Classification (BEC), only sites defined as circum-mesic (01 site series, DeLong 2003) were used, thereby restricting site-specific moisture influences (i.e., soil and/or topographic features).

Mesic sites, referred to as 'zonal sites' in BEC, are areas with average soil and site conditions that best reflect the regional climate (Pojar et al. 1987). Four biogeoclimatic (BGC) subzones are represented in this thesis: 1) very dry cold (xc), 2) dry cool (dk), 3) moist cold (mc), and 4) wet cool (wk) (DeLong 2003). Two sites were sampled from each of these four subzones for a total of eight sites (Table 1).

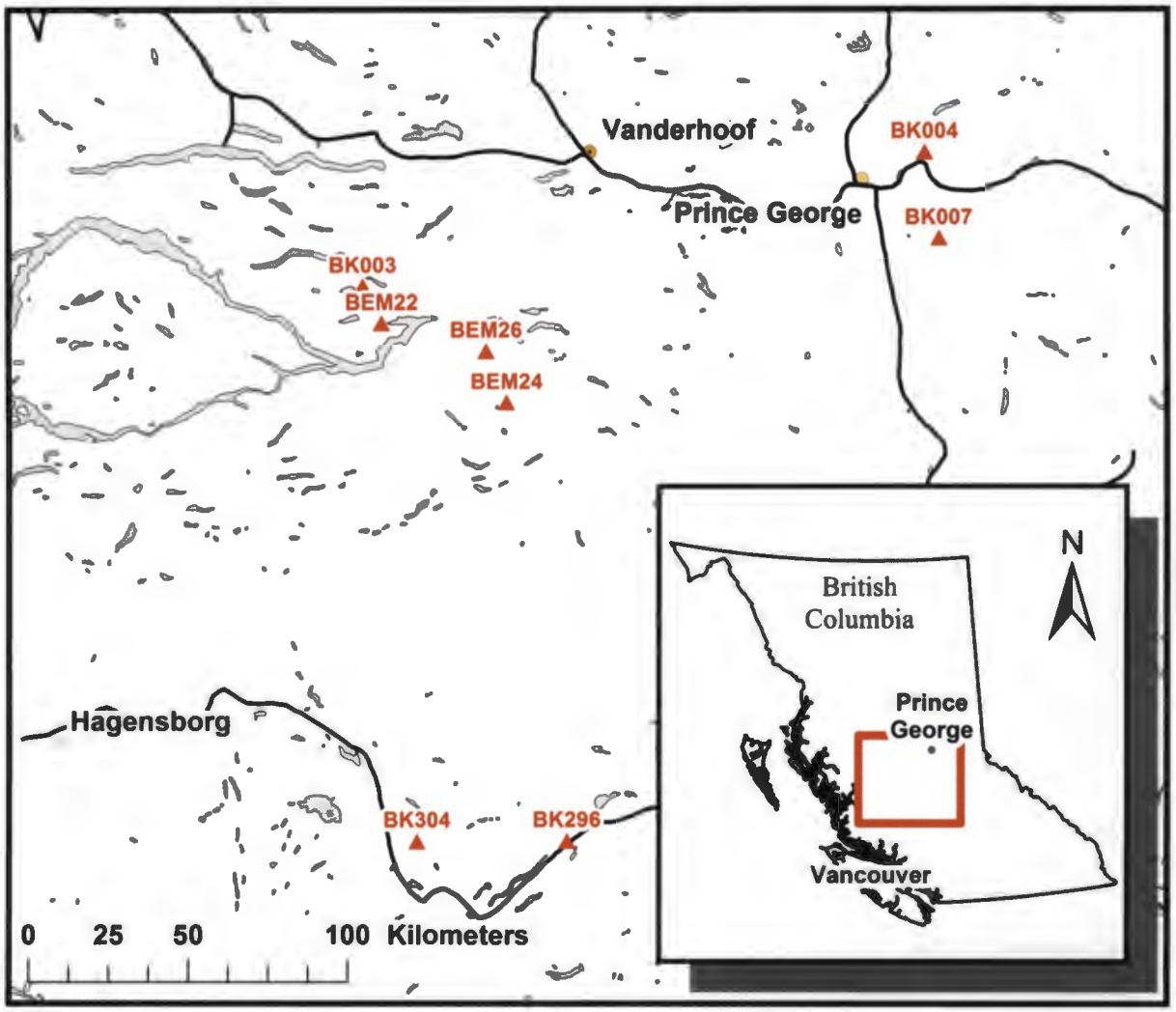


Figure 1. Study area and site locations in the central interior of BC.

Table 1. Study sites and affiliated climate conditions.

Site	BGC unit	Latitude	Longitude	Elevation (m)	MAP (mm)	MAT (°C)
BK304	SBPSxc	52.0906	-124.8890	1252	463	1.1
BK296	SBPSxc	52.0831	-124.2033	947	295	2.6
BK003	SBSdk	53.6512	-125.1063	909	500	2.1
BEM 22	SBSdk	53.5483	-125.0206	920	494	1.9
BEM 26	SBSmc3	53.4630	-124.5266	1061	544	1.3
BEM 24	SBSmc3	53.3203	-124.4353	1146	544	1.0
BK004	SBSwk	53.9781	-122.4056	698	698	3.2
BK007	SBSwk1	53.7370	-122.3594	850	732	2.9

Field sampling

Field work was conducted between August and September 2011. At each site, I selected dead lodgepole pine boles that had evidence of MPB attack; signs included pitch tubes and beetle exit holes in the bark, and linear J-shaped galleries under the bark. Blue stain in the sapwood also aided in confirming MPB-induced mortality. With the help of a field assistant, I collected wedges from snags and live lodgepole pine trees, and disc samples from suspended and down boles. Live lodgepole pine, if found at a site, were sampled to provide a baseline for maximum wood and carbon density.

I used a census-based approach for sampling MPB-killed CWD at each field site. All CWD that met the criteria were included until the target number of boles had been sampled, or site conditions were no longer suitable, whichever came first. For every two fallen boles (suspended

or down CWD) sampled, I sampled one MPB-killed snag[7]. The objective was to sample a similar number of boles in each of the position categories (snags, suspended, and down) for a total of approximately 24 boles per site.

The threshold for classifying CWD as suspended or down was determined on the basis of whether the majority of the bole was greater than 10 cm off the ground (suspended), or not (down). Samples were later individually classified by the same criteria as either suspended or down. Coarse woody debris (suspended or down) was only sampled if the following conditions were met:

- Dimensions $\geq$ 7.5 cm diameter at breast height (DBH, defined as 1.3 m from the base of the tree), and $\geq$ 2 m in unbroken length
- At an angle of $\leq 45°$ from the ground and not self-supporting[8]
- Sufficient evidence to confirm species as lodgepole pine, and MPB impacted
- Presence of an adjacent live 'witness' tree having either a scar inflicted from the fall event, or a curve at the base (i.e., with reaction wood) from being pushed over during the fall event.

Before cutting a log for samples, the bole, and selected sample locations along the bole were characterized by decay class (Maser et al. 1979) and several other micro-site factors (see Appendix B, Table B1). The height of the bole from the ground was measured at each sample location, including negative values for boles imbedded in the forest floor. These values were

[7] Any standing dead tree >1.3 m tall and self-supporting, as defined by Thomas et al. (1979) and BC Ministry of Forests (1998).

[8] A self-supporting bole is only supported by its own roots. A non-self-supporting bole therefore is either resting on the ground, or is held up off the ground by something other than its own roots (e.g., leaning or resting on other standing trees, other logs, its own branches, etc.).

later used to determine the classification of sample position as either suspended or down, as well as characterize the sample position numerically.

The primary sample collection method involved cutting a cross-sectional slice (i.e., cookie) from the main stem of CWD. Samples collected from the witness trees captured either the fall-scar or reaction wood which was then used to date the year of fall of the sample tree (Maser and Trappe 1984, Harmon et al. 1986). I took two cookies from every suspended or down bole to characterize the variability of decay within individual stems. A third cookie was taken to date the year of death of the tree.

Collection of samples from CWD with advanced decay (i.e., decay class 3 or greater, Maser and Trappe 1984, BC Ministry of Forests 1998) was limited by the extent to which I could clearly differentiate the degraded CWD wood from the surrounding organic soil and detrital material, and retain the sample intact for volumetric measuring. For such cases, a section of the log was cut and removed adjacent to the sample in order to observe and measure it without disrupting the log's morphology. If there was evidence of physical fragmentation and loss of volume, un-decayed diameters were inferred, based on the horizontal diameter and the most intact parts of the cross-section that remained. This was not a mathematically-derived correction for volume losses as developed by Fraver et al. (2013); rather, it was a subjective method that allowed estimates to be made based on the condition of individual logs. Highly decayed samples were shrink-wrapped and transported to freezer storage as quickly as possible.

Snags and live trees were sampled by cutting a wedge from the trunk at 1.3 m from the base of the tree[9]. For snags, a core was taken at the same height for dating the tree's year of death.

In the field, maximum and minimum diameters of all cookies were measured and recorded for volumetric calculations. Diameter measurements excluded bark to ensure consistency whether bark was present or not. Cookie thickness was measured at approximately eight points around the perimeter to ensure that the most representative average value was reported. The field data sheet and a list of field parameters are included in Appendix B (Figure B1 and Table B1).

Laboratory analyses

Determination of wood density

Samples were transported to the Enhanced Forestry Laboratory at UNBC in Prince George, BC, and stored at either room temperature (22 °C), in a cooler at 4 °C in burlap sacks, or wrapped in plastic and frozen at -20 °C. All samples with advanced decay were frozen until processing. In the lab, I removed the bark, took photos and weighed each sample.

Basic wood density is defined as oven-dry mass divided by green (i.e., field) volume (Williamson and Weimann 2010). I chose to use field volumes for my density measurements because they would be most representative of the tree's original live dimensions. Two methods were used for measuring cookies: 1) field-volumes were calculated from the geometric measurements recorded in the field (excluding bark), and 2) lab-based volumes were measured by the immersion method described by Graham and Cromack (1982), Williamson and Weimann (2010), and others.

[9] This was the best way I could acquire samples from snags without being qualified to fall trees.

Field volumes were calculated using the equation of a cylinder:

(1)

$$V = \pi \left(\frac{d_{max} + d_{min}}{4} \right)^2 \times (l_{avg})$$

where V is the cookie volume (cm^3), d_{max} and d_{min} are the largest and smallest diameters (cm) of the disc, respectively, and l_{avg} is the average length (cm) or thickness of the cookie.

For lab-based volumes, samples were vacuum sealed in plastic and immersed in a 50 L water tank on an electronic balance. Based on bag weight and density, I calculated the bag volume to subtract from the total displacement volume, thereby reducing measurement error and inflated sample volumes.

The immersion method was used to verify volumes for irregularly-shaped samples including wedges, which were not measurable in the field by geometric means. The volume of oven-dried samples was also measured in order to calculate the amount of shrinkage that occurred from field to oven-dry weight. I then used this shrinkage factor to extrapolate field volumes for wedges, which had lost moisture and presumably volume during storage in the lower-humidity conditions[10].

All samples were dried at 101 °C until constant weight was achieved, as recommended by Williamson and Wiemann (2010). Samples were cooled in large plastic bags with desiccant to

[10] Shrinkage was determined by calculating the percent volume loss that occurred for decay class 1 and 2 samples between field and oven-dried moisture content. The shrinkage that occurred from indoor storage to oven-dry conditions was also measured and subtracted from the field-to-oven shrinkage. The remaining shrinkage factor (4.1 % ± 0.7) represented the volume loss for wedges between field and low-humidity storage conditions. The volume of wedges stored in low-humidity conditions was therefore expanded by the shrinkage correction factor to extrapolate field volumes.

minimize reabsorption of moisture. Oven-dry weights were used with field-based (i.e., green) volumes to calculate basic wood density (Husch et al. 2003, Williamson and Wiemann 2010).

Because of the dependence of wood volume on moisture content (MC), it is important to document the MC at the time of volume measurement. Samples were not readily weighed at the time of collection, so field MC was determined from samples that were stored in the freezer, as these had not lost moisture and volume due to the drier conditions of other storage methods. Samples covering a full range of decay classes had been stored in the freezer, so these provided a means to extrapolate the field moisture content of the other samples.

Carbon concentration analysis

A subsample of 47 cookies covering a range of decay classes was used to evaluate carbon concentration. The first step of grinding samples was completed at the Enhanced Forestry Lab at UNBC in Prince George; this involved grinding each sample in its entirety to a coarse powder using a Micron hammer mill. Complete samples were ground to ensure the carbon analysis would be representative of the full cross section of the bole at the sampling point. All subsequent sample preparation steps and analyses were completed at the Pacific Forestry Centre in Victoria, BC. Using a Humboldt splitter, I divided the ground material of each sample repeatedly until it was reduced to an amount appropriate for further processing (approximately 100 mL). These subsamples were ground with a Retsch cyclone mill and finally with a Retsch ball grinder to obtain an even-textured fine grind of less than 10 μm.

Approximately 5 mg of each sample were used for carbon concentration analysis in a Costech elemental analyzer; an additional amount of the final ground material was concurrently dried at

103 °C overnight to determine the moisture correction factor for each sample. Resultant carbon concentrations were converted to carbon densities by multiplying the concentration data by the respective basic wood density of each sample.

Dendrochronology

All samples for dating the year of death and year of fall of sampled trees were processed and analyzed in the Dendrochronology Lab at UNBC. Increment cores were mounted and sanded using standard dendrochronology techniques (Stokes and Smiley1968). Cookies that were sound were sanded directly without any mounting. Those with evidence of deterioration were mounted on plywood before sanding. Fall-scar and reaction wood samples were sanded and evaluated for the year of fall of all suspended and down boles.

To determine the year of death, annual ring widths were measured to the nearest 0.001 mm using a Velmex System (Velmex, Inc. 1992) and MeasureJ2X software (VoorTech Consulting 2004). Each sample was cross-dated against a master chronology that had been established previously for the same study area (Thompson 2005). Cross-dating was done using a combination of the COFECHA (Holmes 1983) software program and visual cross-dating for verification.

The year of tree fall was determined from fall-scar wedges by counting from the outermost ring (2011) back to the ring in which the damage occurred. For reaction wood samples, the year of tree fall was evident as the ring in which tree growth changed from normal concentric rings to darkened disproportionately thicker growth on only one side of the sample cross-section (i.e., the altered growth of a conifer as it rights itself from being pushed over).

Statistical analyses

Wood density as a means to quantify carbon density

To test if basic wood density can be used as an effective predictor of carbon density, I used simple linear regression. Because carbon density and wood density were correlated by the common unit of sample volume, I ran a second linear regression to evaluate the relationship between C concentration and wood density, which were completely independent parameters. None of the data strayed too far from normal distributions, so assumptions of normality were acceptable.

Carbon density loss from decaying MPB-killed wood

To evaluate if carbon density differed among the position categories of dead standing (snags), suspended, or down boles, I used analysis of variance (ANOVA), followed by Sheffé's test to determine where differences occurred. Samples from live lodgepole pine trees were included as a category in the ANOVA as a baseline for carbon density from which other categories would diverge. To meet the assumption of normality, carbon density data were square-transformed prior to running the ANOVA. Sheffé's test can handle uneven numbers of observations between groups (Tabachnick and Fidell 2001) which was the case with the carbon density data (Appendix C, Table C1). The preliminary ANOVA assessment supported differentiating among the snag, suspended CWD, and down CWD categories, so the remainder of statistical analyses were conducted on these groups independently.

I used linear mixed effects models to account for the hierarchical structure of my study design, which consisted of samples nested in boles, and boles nested within sites. In mixed effects models, the fixed portion of the model includes the parameters of interest (i.e., the fixed effects);

the random effects are variables that are not of interest per se, but may account for variance introduced by sampling different groups within a larger population. The error associated with the random effects is not estimated with that of the fixed effects; rather, it is estimated as a separate component of the overall model error (Rabe-Hesketh and Skrondal 2008). By partitioning the variance among the fixed and random factors, mixed models can explain more of the residual error of a hierarchical study design than a simple regression model (Rabe-Hesketh and Skrondal 2008). The fixed portion of my models consisted of carbon density regressed on the predictor variables (i.e., the fixed effects at level 1); these observations were nested in the random effects of boles (level 2), which were nested within sites (level 3). The formula describing the partitioning of variance for a three-level nested random-intercept model is:

(2)

$$y_{ijk} = \beta + u_{jk}^{(2)} + u_{k}^{(3)} + \epsilon_{ijk}^{(1)}$$

where i = the level 1 observations, j = the level 2 groups (i.e., boles), k = the level 3 groups (i.e., sites) (StataCorp. 2009a). Applied to my study, y_{ijk} is a carbon density observation nested in a bole and site, β is the fixed effects intercept, $u_{jk}^{(2)}$ is the level 2 random intercept for boles nested in sites, $u_{k}^{(3)}$ is the level 3 random intercept for sites, and $\epsilon_{ijk}^{(1)}$ is the level 1 error term associated with individual observations.

To evaluate the influence of the fixed effects, I constructed a set of candidate models for each tree position category that reflected my hypotheses, which were based on empirical observations and evidence from the literature. Candidate models consisted of years since tree death or tree

fall as the main predictor variable, with climate parameters and height off the ground as additional explanatory variables (see Table C2 in Appendix C for a summary of all potential predictor variables).

I used four different potential climate variables to evaluate which, if any, best explained the variation in the data; these were 1) MAP and MAT, 2) mean winter (January, February, and December precipitation and temperature, 3) mean summer (June, July, and August) precipitation and temperature, and 4) BEC subzones. The four types of climate variables were chosen for the following reasons: MAP and MAT are commonly used climate predictors and are therefore useful for comparing with other studies, and potentially for extending results to other locations. Because of the reported importance of January and July climate parameters as significant predictors of wood decay by Yin (1999), I included average winter or summer precipitation and temperature data as more specific alternatives to MAP and MAT. Both the mean annual and seasonal climate data were interpolated using the online version of ClimateWNA (Wang et al. 2012). BEC subzones provide another means of describing climatic differences between sites by incorporating climate and other ecological factors into ecosystem-specific classification units (Meidinger et al. 1991); I therefore used BEC subzones as a fourth and simpler option that grouped sites into one of four climatic categories (very dry cold, dry cool, moist cold, and wet cool).

To evaluate which of the candidate models best described changes in carbon density, I used Akaike's Information Criterion (AIC) for small datasets (AIC_c; Burnham and Anderson 2002). Information theoretic approaches such as AIC follow the principle of parsimony: models are ranked to balance the benefits of improving the explained variance against the costs of including

more parameters in a model (Gotelli and Ellison 2004). Models that explain more of the variance with fewer parameters have a lower AIC score. Therefore, the best model out of a given set of candidates is identified by the lowest AIC score. If a candidate model ranks within 2 AIC units of the best model, it is often considered to explain a comparable proportion of the observed variance as the top-ranked model (Burnham and Anderson 2002). In some cases, parameter coefficients of the top-ranking models can be averaged to yield a single, best-fitting model. However, averaging may not always be the preferred route to describe the system being modelled; in the case of complex systems, multiple models of similar explanatory value but differing parameters may be more realistic. For this reason, I reported all models ranking within 2 AIC_c units of the top model.

To enable the comparison of the relative influence of predictors on carbon density, I plotted standardized versions of the coefficients from the top-ranking models. This was done by scaling and centering the predictor variables, which accounted for the different units with which they were quantified. To maintain interpretability, I reported only the raw unstandardized coefficients, which therefore related directly to the units of both carbon density and each respective predictor variable.

I checked model validity by evaluating the assumptions of linear mixed effects regression models. The residuals were normally distributed, but there were some issues of multicollinearity for the predictor variables. In these cases, I ran the model again without the variable causing the collinear issue (Tabachnick and Fidell 2001). Influential points were inspected and in most cases determined to be within the reasonable bounds of the dataset. Any dubious outliers were omitted. All analyses were performed using Stata 11 (StataCorp 2009b). Figures were generated

using Stata (StataCorp 2009b), Microsoft Excel 2010 (Version 14.0.7166.5000), and Microsoft PowerPoint (Version 14.0.7166.5000).

RESULTS

Wood density as a means to quantify carbon density

Across the range of observed wood decomposition, wood density was a very good predictor of carbon (C) density ($r^2 = 1.00$, $p < 0.001$, n=47). Carbon density decreased by 0.4996 g cm^{-3} for every 1 g cm^{-3} decrease of wood density (Table 2, Figure 2). This relationship is described by the equation:

$$d_C = 0.4996 \times d_w + 0.0043$$

where d_c is the density of carbon (g C cm^{-3} sample), 0.4996 is the slope, d_w is the basic density of wood (g wood cm^{-3} sample), and 0.0043 is the y-intercept.

Table 2. Linear regression coefficients for carbon density versus wood density, and carbon concentration versus wood density.

(n=47)	coefficient	standard error	p-value	95 % confidence interval
carbon density versus wood density:				
Wood density	0.4996	0.00339	<0.001	0.492 – 0.506
carbon concentration versus wood density:				
Wood density	-0.05707	0.0102	<0.001	-0.0776 – -0.0365

Wood density was also a good predictor of carbon concentration ($r^2 = 0.41$, $p < 0.001$, n=47). For every 1 g cm^{-3} of wood density lost (Figure 3, right to left), carbon concentration increased by 0.057 g C g^{-1} of wood (Table 2). The concentration of carbon in wood samples was slightly

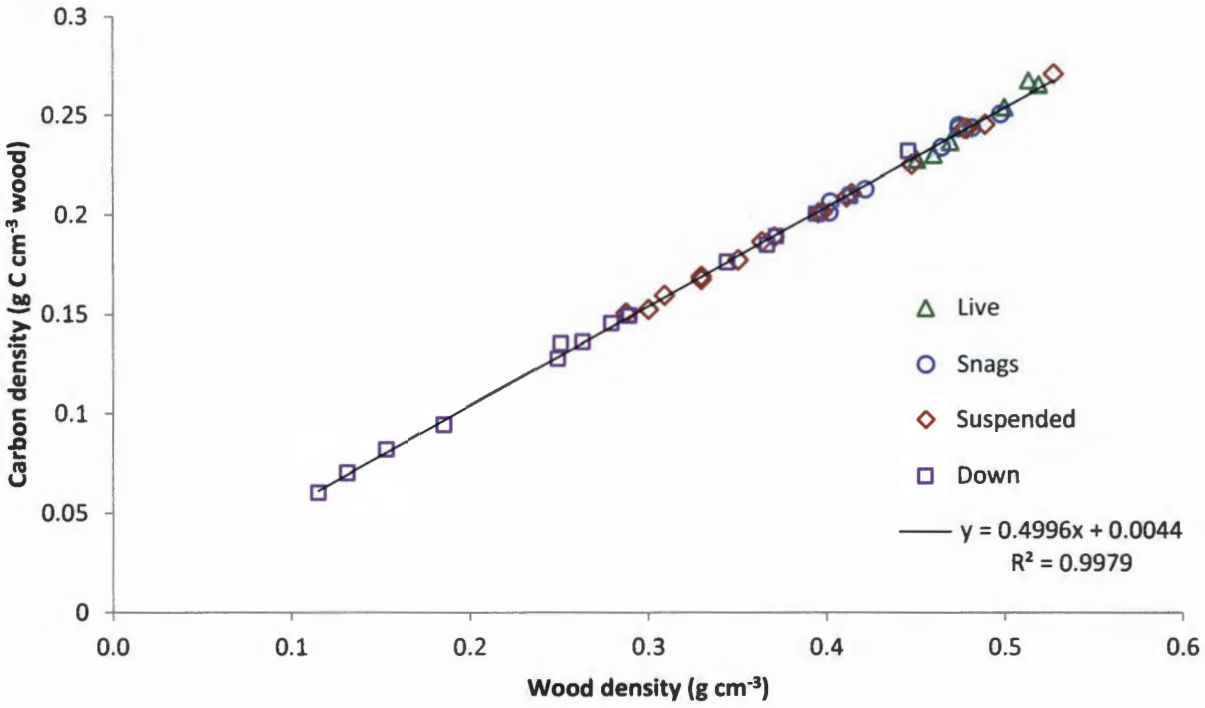


Figure 2. The relationship between carbon density and wood density for all categories of lodgepole pine samples, with a best-fitting trend line.

higher at lower wood density values (i.e., higher carbon concentration with increasing decay), although there were fewer data representing this end of the spectrum (Figure 3).

The second regression demonstrated the relative stability of carbon concentration within the range of observed wood densities. Basic wood density ranged from 0.48 g cm^{-3} down to 0.11 g cm^{-3}, which represented a loss of about 76 % of the initial wood density. In contrast, over this broad range of wood density, carbon concentration remained relatively constant, within a margin of 7.5 % (from 0.50 to 0.54 g C g^{-1} wood) (see Table C1 in Appendix C for wood and carbon densities of the full dataset, with carbon concentrations for comparison).

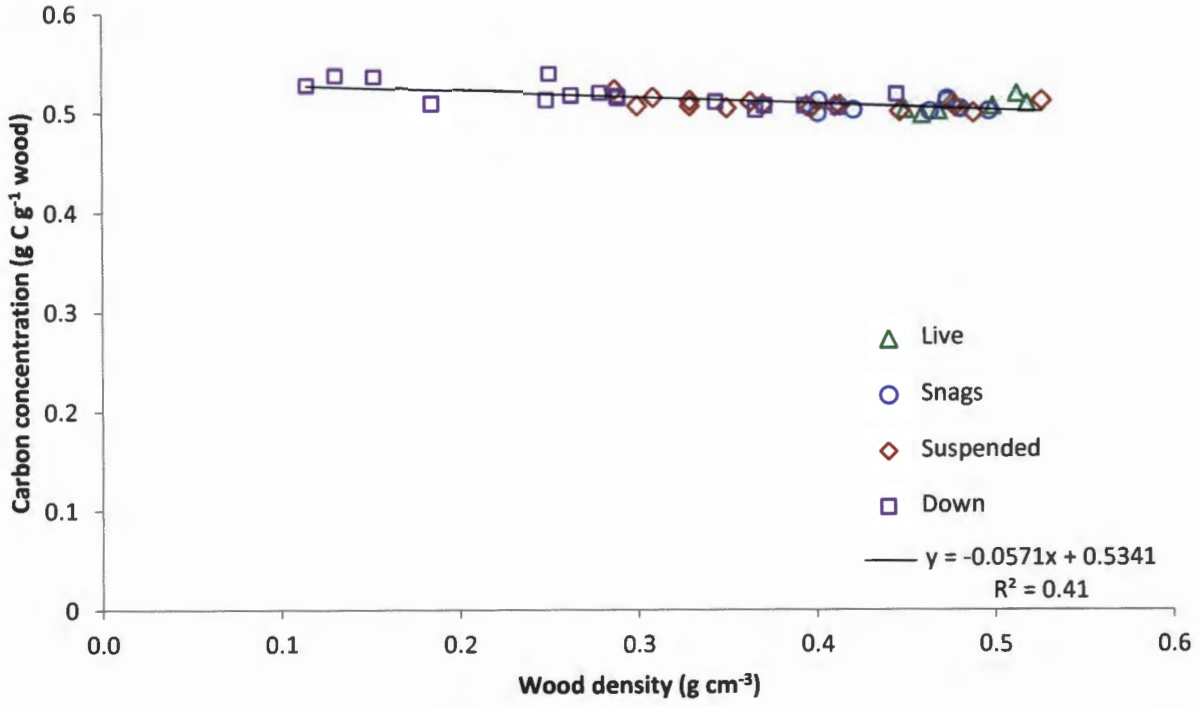


Figure 3. Relationship between carbon concentration and wood density for all categories of lodgepole pine.

Carbon density loss from decaying MPB-killed wood

Carbon density by position categories

Mean carbon density of samples from suspended and down MPB-killed CWD was significantly lower than that of live lodgepole pine or upright MPB-killed snags (Table 3). Suspended and down CWD were also significantly different from each other, with the latter having the lowest average carbon density. Carbon density of snags did not differ from that of live lodgepole pine (Table 3), although the range of observed carbon density was larger for snags (Figure 4). Live lodgepole pine trees, which were sampled to provide a baseline starting point of carbon density for decayed boles, had a mean carbon density of 0.247 (± 0. 014) g C cm^{-3} of sample wood (Table 3).

Table 3. Scheffé's test comparing mean carbon density for position categories, including live wood as a baseline maximum. Different superscripted lowercase letters indicate significant differences.

Tree category	n	Mean C density ($g\ C \cdot cm^{-3}$)	St. err.	95 % CI
Live	10	0.247^{a}	0.004	0.237 – 0.257
Snags	45	0.225^{a}	0.003	0.218 – 0.231
Suspended	116	0.196^{b}	0.003	0.191 – 0.202
Down	69	0.161^{c}	0.007	0.148 – 0.175

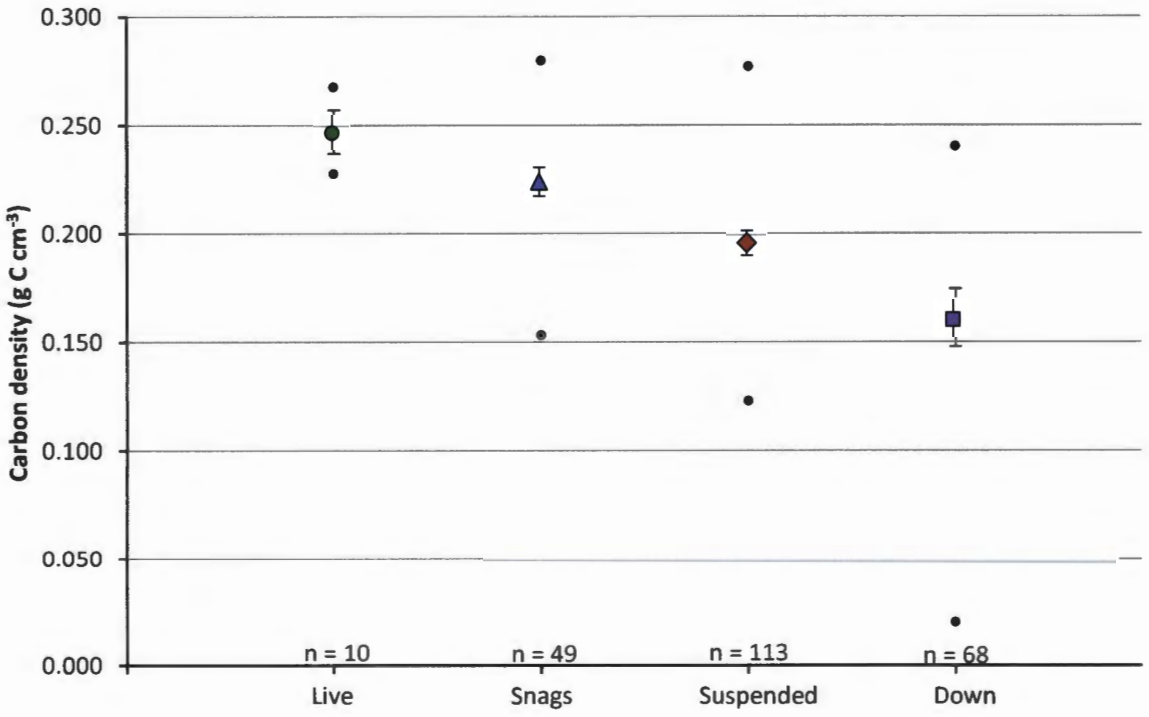


Figure 4. Mean carbon density ± standard error for dead-tree position categories, with live-tree carbon density as a baseline for comparison. Minimum and maximum observations for each category are indicated with dots.

The variance of carbon density was greater within tree position categories than it was among them (Table 4), and the within-group variability increased with each category as evidenced by the maxima and minima for snags, suspended, and down boles, respectively (Figure 4, see also Appendix C, Figure C1 for the variability in raw data by position categories).

Table 4. ANOVA comparison of carbon density by position categories.

	SS	MS	df	F	Prob > F
Among groups	0.147	0.049	3	35.13	<0.0001
Within groups	0.330	0.001	236		
Total	0.478	0.002			

Best candidate models and predictors of carbon loss

Snags

For snags, the 'null' model ranked highest, which indicated that none of the candidate models explained an appreciable amount of the observed variance of carbon density compared to a model with no explanatory predictors (Table 5). The lack of correlation between carbon density and the predictor variables considered suggests that none of these factors strongly influence the loss of carbon in snags (Appendix D, Figure D1). In other words, the carbon density of snags remains relatively constant over time, regardless of the variability in mean annual or seasonal precipitation and temperature.

Table 5. Candidate models and AIC_c ranking for snags. The null model ranked highest, and no other models ranked within ≤ 2 ΔAIC_c scores of the null model. Random effects are italicized.

Candidate models for snags (n=43):*	Model#	K	AIC_c	ΔAIC_c
Null model: *site*	**01**	**3**	**-195.4**	**0**
yrsdead+*site*	11	4	-193.0	2.4
yrsdead+MAP+MAT+*site*	21	6	-190.1	5.3
yrsdead+PPTwt+Twt+*site*	22	6	-191.8	3.6
yrsdead+PPTsm+Tsm+*site*	23	6	-189.9	5.5
yrsdead+BEC4+*site*	24	5	-193.1	2.3
yrsdead+MAP+MAT+yrsdead*MAP+*site*	41	7	-187.6	7.8

*Model parameter definitions: yrsdead = years dead, MAP = mean annual precipitation (mm), MAT = mean annual temperature (°C), PPTwt = mean winter precipitation (mm), Twt = mean winter temperature (°C), PPTsm = mean summer precipitation (mm), Tsm = mean summer temperature (°C), BEC4 = biogeoclimatic ecosystem classification with 4 subzone categories.

The random effect of site was included in all models[11] for snags, which accounted for a very small portion of the observed variance. In all cases, the within-site variance was greater than the between-site variance. Regression coefficients for the null model are provided in Table D1, Appendix D.

Suspended CWD

For suspended CWD, sample height off the ground, mean summer precipitation and temperature, and years dead were all good predictors of carbon density. None of the candidate models containing years down, mean annual or mean winter climate variables, or BEC subzones ranked highly (Table 6). The top two models contained the same suite of predictors, with the second-best model including the addition of an interaction term for years dead and mean summer

[11] Samples were nested directly in sites as the random effect for the snag category because only one sample was taken per snag.

precipitation (Table 7). The benefit of adding the interaction term in the second-best model did not outweigh the cost of adding another parameter.

Table 6. Candidate models and AIC_c ranking for suspended CWD. Top-ranked models have ΔAIC_c scores within ≤ 2 of the best model (highlighted in bold). Random effects are italicized.

Candidate models for suspended CWD (n=99):*	Model#	K	AIC_c	ΔAIC_c
Null model: *site+bole*	01	4	-416.2	22.8
yrsdead+*site+bole*	11	5	-424.6	14.3
yrsdown+*site+bole*	12	5	-423.7	15.2
yrsdead+selev+*site+bole*	21	6	-430.9	8
yrsdead+selev+MAP+MAT+*site+bole*	22	8	-436.4	2.6
yrsdead+selev+PPTwt+*site+bole*†	23	7	-434.6	4.3
yrsdead+selev+PPTsm+Tsm+*site+bole*	**24**	**8**	**-438.9**	**0**
yrsdead+selev+BEC4+*site+bole*	25	7	-430.4	8.6
yrsdown+selev+*site+bole*	31	6	-428.7	10.3
yrsdown+selev+MAP+MAT+*site+bole*	32	8	-433.4	5.6
yrsdown+selev+PPTwt+Twt+*site+bole*	33	8	-434.3	4.6
yrsdown+selev+PPTsm+Tsm+*site+bole*	34	8	-434.7	4.2
yrsdown+selev+BEC4+*site+bole*	35	7	-427.7	11.3
yrsdead+selev+MAP+MAT+yrsdead*MAP+*site+bole*	41	9	-436.0	3.0
yrsdead+selev+PPTsm+Tsm+yrsdead*PPTsm+*site+bole*	**42**	**9**	**-437.2**	**1.7**

*Model parameter definitions are the same as in Table 5, with the addition of: yrsdown = years down, and selev = sample elevation (cm).

†Winter temperature dropped from candidate model for multicollinearity issues.

Table 7. Regression coefficients of top-ranked linear mixed models for MPB-killed lodgepole pine CWD in a suspended position. Continued next page.

model 1	Coeff.	St. Err.	95 % C. I.
fixed effects:*			
years dead	**-0.000551**	**0.000183**	**-0.000910 – -0.000192**
sample elevation	**0.000442**	**0.000121**	**0.000205 – 0.000680**
precipitation$_{(s)}$	**-0.000369**	**0.0000902**	**-0.000546 – -0.000192**
temperature$_{(s)}$	**0.00764**	**0.00318**	**0.00141 – 0.0139**
(intercept)	0.138	0.0394	0.0608 – 0.215
random effects:			
site	4.86×10^{-10}	4.05×10^{-09}	3.97×10^{-178} – 0.00595
boles (nested in sites)	0.0150	0.00353	0.00943 – 0.0237
st. dev. (residual)	0.0196	0.00229	0.0156 – 0.0247

* Definitions and units: sample elevation (cm), precipitation$_{(s)}$ = mean summer precipitation (mm), temperature$_{(s)}$ = mean summer temperature (°C).

In both top-ranking models for suspended CWD, sample elevation had the greatest influence on carbon density, followed by mean summer precipitation, years dead, and mean summer temperature (Figure 5). Sample elevation and mean summer temperature were positively correlated with carbon density (Table 7). Summer precipitation and years dead both had negative associations with carbon density. The interaction term for years dead and summer precipitation was generally positive, meaning higher precipitation over time yielded greater loss of carbon density, but the pattern was not consistently positive for all cases (Figure 5).

With all other parameters in the best-ranked model held steady, carbon density was 0.000442 ± 0.000238 g cm^{-3} greater for every centimeter of sample height off the ground (Table 7).

Table 7 continued. Regression coefficients of top-ranked linear mixed models for MPB-killed lodgepole pine CWD in a suspended position.

model 2	Coeff.	St. Err.	95 % C. I.
fixed effects:*			
years dead	-0.00113	0.000716	-0.00254 – 0.000269
sample elevation	**0.000453**	**0.000121**	**0.000214 – 0.000691**
precipitation$_{(s)}$	**-0.000473**	**0.000153**	**-0.000772 – -0.000174**
temperature$_{(s)}$	**0.00734**	**0.00319**	**0.00110 – 0.0136**
years dead * precip$_{(s)}$	5.09×10^{-06}	6.04×10^{-06}	-6.74×10^{-06} – 0.0000169
(intercept)	0.154	0.0434	0.0686 – 0.239
random effects:			
site	6.48×10^{-10}	6.90×10^{-09}	5.57×10^{-19} – 0.753
boles (nested in sites)	0.0148	0.00393	0.00881 – 0.0249
st. dev. (residual)	0.0196	0.00293	0.0146 – 0.0263

* Definitions and units: sample elevation (cm), precipitation$_{(s)}$ = mean summer precipitation (mm), temperature$_{(s)}$ = mean summer temperature (°C).

In other words, carbon density was 0.18 ± 0.096 % closer to that of live lodgepole pine with every centimeter of sample elevation off the ground. Likewise, for every millimeter increase in mean summer precipitation, carbon density decreased by -0.000369 ± 0.000177 g C cm^{-3} (-0.15 ± 0.071 % of live lodgepole pine carbon density). Suspended boles lost carbon density at a rate of -0.000551 ± 0.000359 g C cm^{-3} per year. This is equivalent to an average loss of -0.22 ± 0.074 % carbon density per year, as represented by these data for the 70-year period following tree death. Carbon density was 0.00764 ± 0.00624 g C cm^{-3} (3.09 ± 2.52 %) higher for every increase of 1 °C (Table 7).

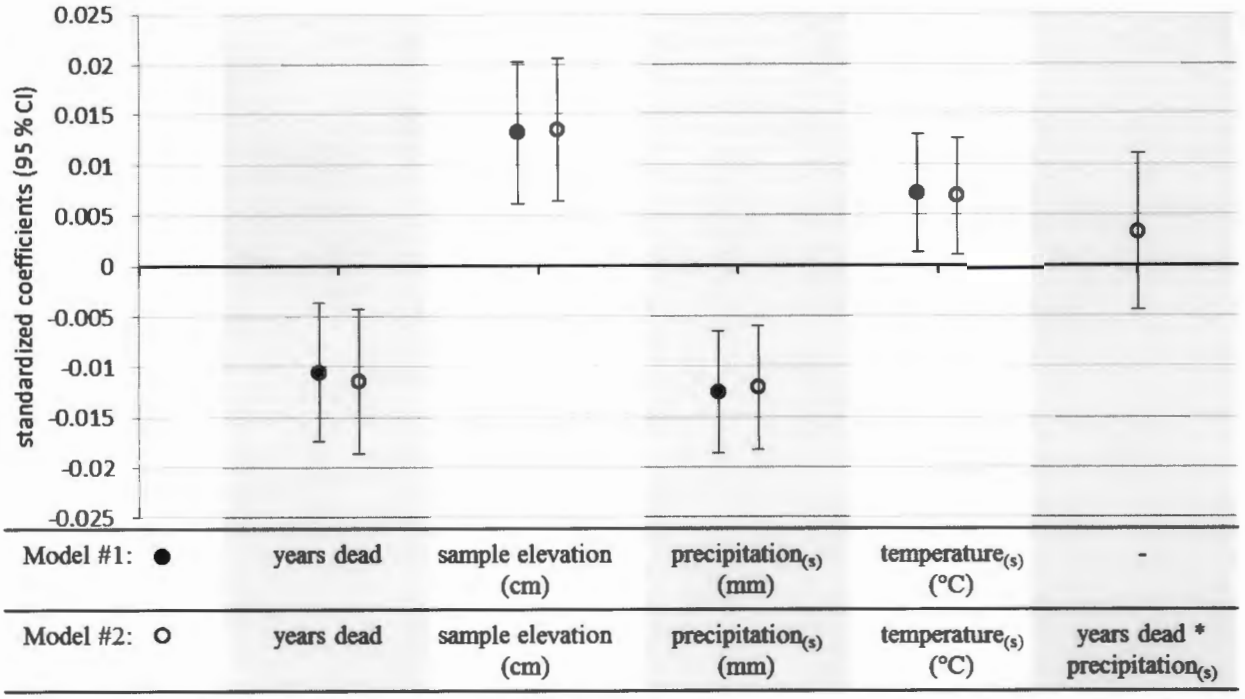


Figure 5. Standardized coefficients (with 95 % C.I.) of the top-ranked models for carbon density in suspended CWD. The further a standardized coefficient is from zero, the better predictor it is of carbon density. Sample elevation had the greatest relative effect on carbon density, followed by summer precipitation, years dead, and summer temperature. The confidence interval for the interaction term in model #2 included zero and was therefore not a strong predictor.

The range of mean summer temperature across the study area was only 3.3 °C (11 to 14.3 °C), so the relative effect of temperature on carbon density was small compared to other parameters, despite the impression given by a high percentage rate of change per °C (Figure 5 illustrates the relative influence of the predictor variables on carbon density in the top candidate models for suspended CWD).

Down CWD

For down CWD, four candidate models ranked within 2 scores of $\Delta AIC_c = 0$ (Table 8), and each of these four models included years down as a leading predictor variable. Sample elevation and years down were the only predictors of carbon density in the top-rated model. Sample elevation and years down therefore explained more variance together than the combination of predictors in the subordinate-ranking models. Years down, sample elevation, and mean winter precipitation and temperature were explanatory variables in the second and third ranking models. Model #3 also included an interaction term between years down and winter precipitation, but this term did not improve the amount of explained variance beyond the cost of an additional parameter. The fourth-ranked model had only years down as the sole predictor variable. Years dead, mean annual and mean summer climate variables, and BEC subzones were all excluded from the best-ranked models (Table 8), suggesting that none of these predictors explained appreciable amounts of the observed variance in carbon density for down CWD.

Sample elevation was the best predictor of carbon density in down CWD for all models in which it occurred. Mean winter temperature was the second-best predictor, followed by years down (Figure 6). Sample elevation and mean winter temperature were both positively affiliated with carbon density. Years down and mean winter precipitation were negatively associated with carbon density, although precipitation did not consistently have a negative association. The interaction term of years down and winter precipitation was generally positive, meaning the negative effect of one amplified the negative effect of the other, but the pattern was inconsistent.

Table 8. Candidate models and AIC_c ranking for down CWD. Top-ranked models have ΔAIC_c scores within ≤ 2 of the best model (highlighted in bold). Random effects are italicized.

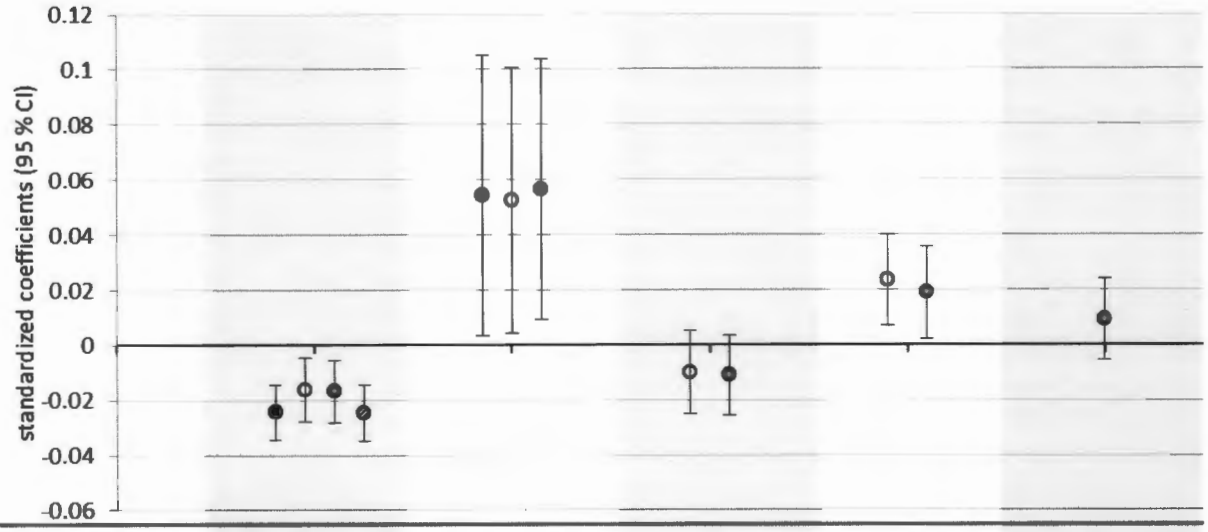
Candidate models*	Model#	K	AIC_c	ΔAIC_c
Down boles (n=56):				
Null model: *site+bole*	01	4	-178.7	16.9
yrsdead+*site+bole*	11	5	-185.0	10.6
yrsdown+*site+bole*	**12**	**5**	**-193.9**	**1.7**
yrsdead+selev+*site+bole*	21	6	-186.5	9.1
yrsdead+selev+MAP+MAT+*site+bole*	22	8	-181.3	14.3
yrsdead+selev+PPTwt+*site+bole*†	23	7	-184.0	11.6
yrsdead+selev+PPTsm+Tsm+*site+bole*	24	8	-181.2	14.4
yrsdead+selev+BEC4+*site+bole*	25	7	-183.9	11.7
yrsdown+selev+*site+bole*	**31**	**6**	**-195.6**	**0**
yrsdown+selev+MAP+MAT+*site+bole*	32	8	-190.6	5
yrsdown+selev+PPTwt+Twt+*site+bole*	**33**	**8**	**-194.9**	**0.7**
yrsdown+selev+PPTsm+Tsm+*site+bole*	34	8	-190.3	5.3
yrsdown+selev+BEC4+*site+bole*	35	7	-193.1	2.5
yrsdead+selev+MAP+MAT+yrsdead*MAP+*site+bole*	41	9	-179.1	16.5
yrsdown+selev+PPTwt+Twt+yrsdown*PPTwt+*site+bole*	**42**	**9**	**-194.8**	**0.8**

*Model parameter definitions are the same as in Table 5, with the addition of: yrsdown = years down, and selev = sample elevation (cm).

†Winter temperature dropped from candidate model for multicollinearity issues.

In the top-ranked model for down CWD, carbon density was 0.00182 ± 0.00170 g cm^{-3} higher for every centimeter of elevation off the forest floor (Table 9). This translated to a loss of -0.74 ± 0.65 % carbon density for every centimeter that a bole was closer to or sinking into the duff. Down CWD lost carbon density at a rate of -0.00298 ± 0.0012 g C cm^{-3} yr^{-1} since tree fall; this

was equivalent to a loss of -1.21 ± 0.27 % carbon density per year. In the second-ranked model, higher mean winter temperatures were affiliated with higher carbon density by a margin of 0.0422 ± 0.0298 g cm^{-3}, or 17.1 ± 12.1 % for every 1 °C increase in temperature (Table 9).



Model #1: ●	years down	sample elevation (cm)	-	-	-
Model #2: ○	years down	sample elevation (cm)	precipitation$_{(w)}$ (mm)	temperature$_{(w)}$ (°C)	
Model #3: ●	years down	sample elevation (cm)	precipitation$_{(w)}$ (mm)	temperature$_{(w)}$ (°C)	years dead * precipitation$_{(w)}$
Model #4: ⊘	years down	-	-	-	-

Figure 6. Standardized coefficients (with 95 % C.I.) of the four top-ranked models for carbon density in down CWD. Sample elevation had the greatest relative influence on carbon density, followed by years down, and mean winter temperature. Mean winter precipitation included zero and was therefore a less reliable predictor, as was the interaction term in model #3.

The effect of mean winter temperature appeared large, but the range across the study area was only 2.5 °C (-8.9 to -6.4 °C); therefore, the coefficient affiliated with temperature described the variance in only 2.5 units, whereas the coefficients of other predictors expressed the variance over broader ranges (e.g., 23 cm for sample elevation, 32 for years down). Once standardized, however, the effect of temperature relative to the other predictors was not large (Figure 6).

Table 9. Regression coefficients of top-ranked linear mixed models for MPB-killed lodgepole pine CWD resting on the ground. Continued next page.

Model #1	Coeff.	St. Err.	95 % C. I.
fixed effects:*			
years down	**-0.00298**	**0.000622**	**-0.00420 – -0.00176**
sample elevation	**0.00182**	**0.000869**	**0.000121 – 0.00353**
(intercept)	0.193	0.0112	0.171 – 0.215
random effects:			
site	0.0200	0.00858	0.00859 – 0.0464
boles (nested in sites)	0.0121	0.0152	0.00103 – 0.142
st. dev. (residual)	0.0323	0.00612	0.0223 – 0.0468
Model #2			
fixed effects:*			
years down	**-0.00198**	**0.000737**	**-0.00342 – -0.000537**
sample elevation	**0.00176**	**0.000824**	**0.000143 – 0.00337**
$\text{precipitation}_{(w)}$	-0.000161	0.000124	-0.000405 – 0.0000826
$\text{temperature}_{(w)}$	**0.0422**	**0.0152**	**0.0124 – 0.0720**
(intercept)	0.523	0.122	0.283 – 0.763
random effects:			
site	1.08×10^{-12}	1.38×10^{-11}	1.50×10^{-23} – 0.0783
boles (nested in sites)	0.0191	0.0124	0.00537 – 0.0682
st. dev. (residual)	0.0306	0.00799	0.0183 – 0.0540

*Definitions and units: sample elevation (cm), precipitation(w) = mean winter precipitation (mm), temperature(w) = mean winter temperature (°C).

Table 9 continued. Regression coefficients of top-ranked linear mixed models for MPB-killed lodgepole pine CWD resting on the ground.

Model #3	Coeff.	St. Err.	95 % C. I.
fixed effects:*			
years down	**-0.00469**	**0.00175**	**-0.00812 – -0.00126**
sample elevation	**0.00190**	**0.000810**	**0.000312 – 0.00349**
precipitation$_{(w)}$	**-0.000345**	**0.000163**	**-0.000665 – -0.0000246**
temperature$_{(w)}$	**0.0342**	**0.0153**	**0.00418 – 0.0643**
years down*precip.$_{(w)}$	0.0000185	0.000011	-3.03×10^{-06} – 0.0000401
(intercept)	0.490	0.119	0.257 – 0.724
random effects:			
site	6.95×10^{-11}	6.33×10^{-10}	1.22×10^{-18} – 0.00397
boles (nested in sites)	0.0166	0.0103	0.00494 – 0.0560
st. dev. (residual)	0.0309	0.00578	0.0214 – 0.0446
Model #4			
fixed effects:			
years down	**-0.00303**	**0.000640**	**-0.00428 – -0.00177**
(intercept)	0.193	0.0117	0.170 – 0.216
random effects:			
site	0.0217	0.00894	0.00969 – 0.0487
boles (nested in sites)	0.00989	0.0193	0.000215 – 0.0455
st. dev. (residual)	0.0342	0.00634	0.0237 – 0.0491

*Definitions and units: sample elevation (cm), precipitation$_{(w)}$ = mean winter precipitation (mm), temperature$_{(w)}$ = mean winter temperature (°C).

DISCUSSION

Wood density as a means to quantify carbon density

The strong relationship between wood density and carbon density supports the use of wood density as a reliable measure of carbon loss from decaying lodgepole pine wood. For the range of wood densities represented by the data (i.e., up to 80 % of total wood density lost), carbon concentrations remained relatively stable. This stability of carbon concentration across the observed spectrum of wood decomposition affirms the predictive capacity of wood density, and supports its use in lieu of carbon content analysis.

The slight increase in carbon concentration at lower wood densities is consistent with the findings for other temperate and boreal conifer species. Preston et al. (1998, 2006) and Hishinuma et al. (2015) reported increasing carbon concentration with higher decay classes for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) *menziesii* Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg), and western red cedar (*Thuja plicata* (Donn.)) on Vancouver Island, BC, and in Japan. Similarly, Norway spruce (*Picea abies* L. Karst), Scots pine (*Pinus sylvestris* L.), and birch (*Betula pendula* Roth and *B. pubescens* Ehrh) in Sweden (Sandström et al. 2007) and Estonia (Köster et al. 2015) showed the same trend. Sakai et al. (2012) found that dead wood of Japanese cedar (*Cryptomera japonica*) D. Don. increased in carbon concentration with advanced decay, but Japanese cypress (*Chamaecyperus obtusa* Sieb. Et Zucc.) Endl. did not.

The trend of increasing carbon concentration with advanced decay is attributable to the cell wall chemistry of wood, as well as to the fungal groups that dominate different phases of decomposition. Lodgepole pine wood is composed of approximately 43 % cellulose, 32 %

hemicellulose, and 25 % lignin (Koch 1996), and the corresponding carbon content in each of these is approximately 44 % (McGinnis and Shafizadeh 1991), 40 % (Whistler and Chen 1991), and 64 % (Chen 1991, Karmanov et al. 2014), respectively. Therefore, decomposition processes that favour one or two of these components can lead to a shift in the overall carbon concentration, as was observed in this study.

Of the two main fungal groups, white-rot fungi are capable of metabolizing lignin, cellulose, and hemicellulose indiscriminately. Brown rots are not able to break down carbon-rich lignin, and by selectively consuming cellulose and hemicellulose, brown rot fungi leave a lignin-rich residual that is consequently higher in carbon concentration (Preston et al. 2006). White rots are often the primary colonizers of dead wood (Schilling et al. 2015), and as a result, carbon concentrations have been shown to remain more or less stable in early phases of decay (Preston et al. 1998). Higher brown rot activity typically becomes more apparent in later phases of decomposition, bringing about a shift to higher lignin and carbon concentrations. In contrast, van der Val et al. (2007) and references therein suggested the opposite pattern: initial colonization by fungi that can exploit easily-accessible cellulose and hemicellulose, followed by later dominance of lignin-degrading fungi.

My results are consistent with a pattern of white-rot dominance in early stages of decay, and higher brown-rot activity in later stages. This trend suggests that the sequence of fungal colonization for MPB-killed lodgepole pine is generally typical of other temperate and boreal softwood species (Preston et al. 1998 and 2006, Sandström et al. 2007), and that the presence of blue-stain fungi introduced by MPB does not cause a divergence from this degradation pathway.

Carbon density loss from decaying MPB-killed wood

For each of the position categories of MPB-killed lodgepole pine, a unique set of predictor variables described the loss of carbon density, except in the case of snags, for which carbon density was not well described by any of the predictor combinations considered. For both suspended and down CWD, sample elevation was the best predictor of carbon density, but this was the only factor in common between the two groups (Figure 7). Elements of time and climate were important predictors for decay in suspended and down CWD, but different iterations of these influences and their magnitudes revealed distinct conditions operating for the two fallen position categories.

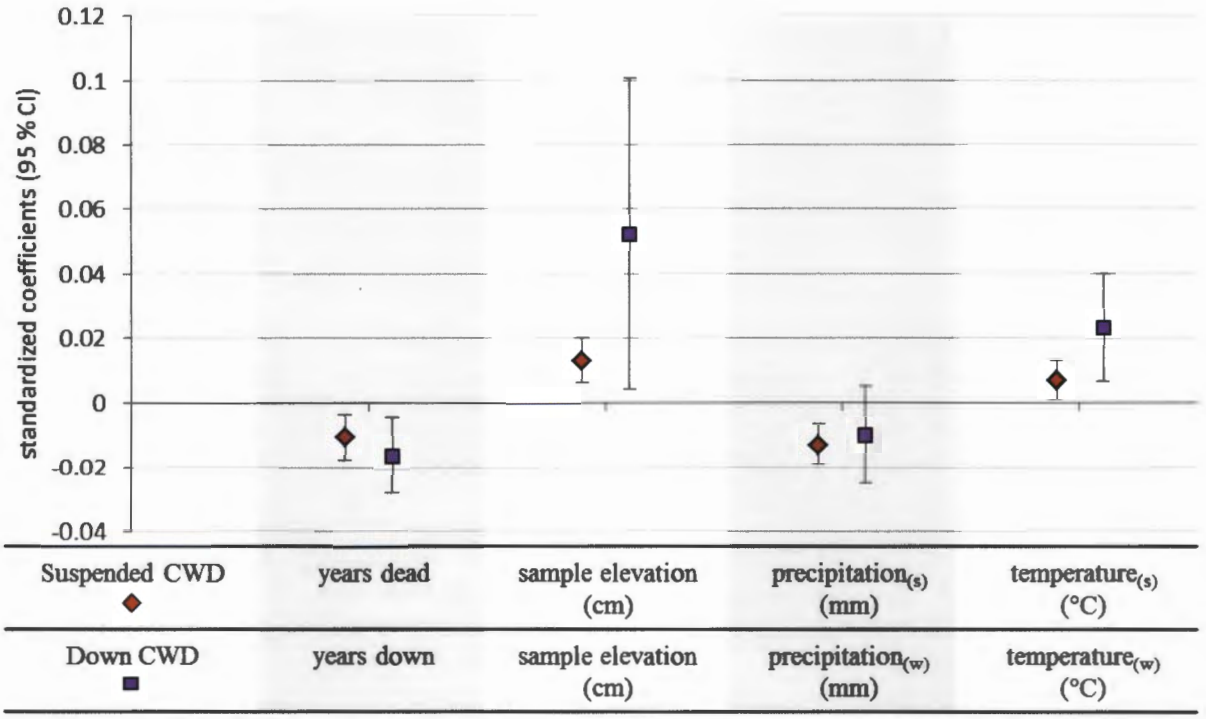


Figure 7. Relative influences of best predictor variables (with 95 % C.I.) for suspended and down CWD. Coefficients are standardized for comparability. Note that the predictors of carbon density loss are different for the two position categories with the exception of sample elevation (e.g., years dead versus years down, and summer versus winter climate variables).

Suspended and down CWD

Effect of position

With all other model predictors held steady, the decline in carbon density was about four times greater for down CWD than for suspended CWD (0.74 % and 0.18 %, respectively) for every centimeter closer that a bole was to the soil, or deeper that it was embedded into the duff (Figure 8). This observation supports the hypothesis that the position of dead boles is an important factor controlling the influence of agents of decay.

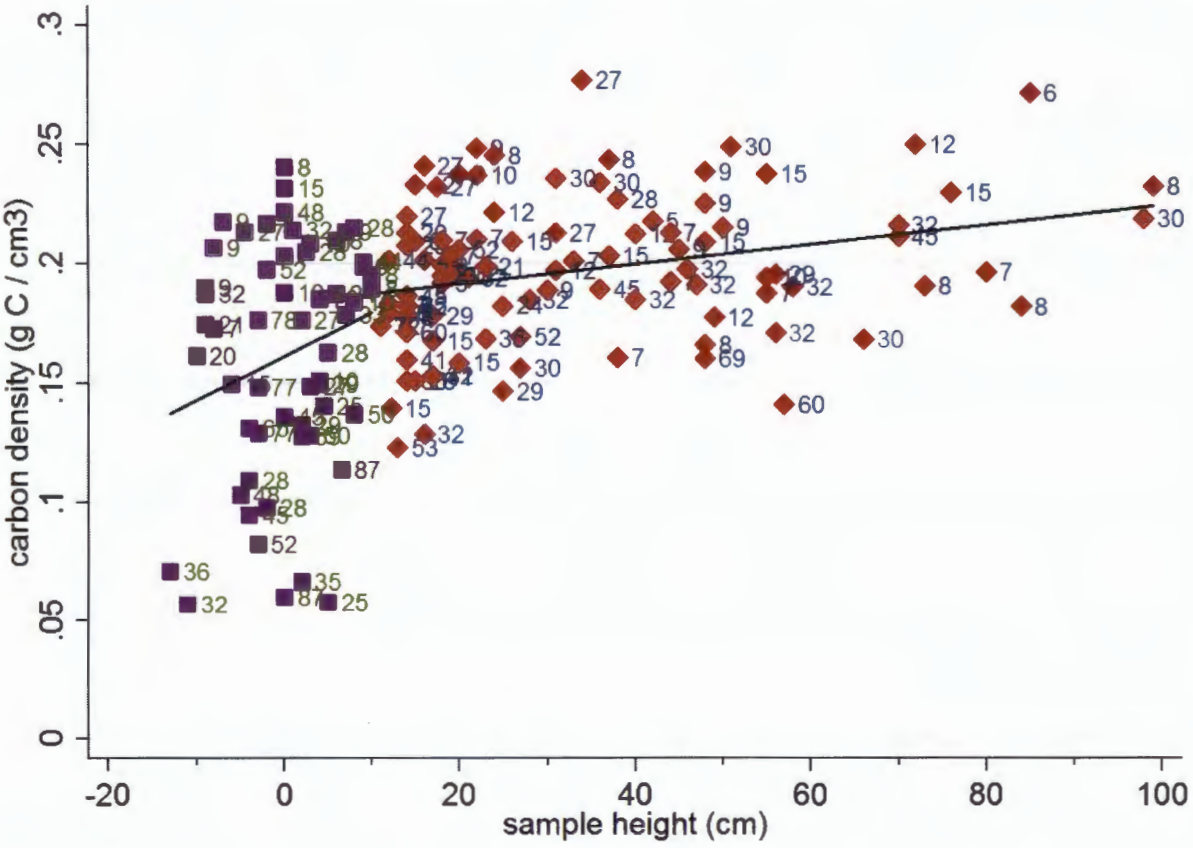


Figure 8. Carbon density (g C cm^{-3}) loss with decreasing sample height off ground (right to left) for suspended CWD (> 10 cm height, red diamonds) and down CWD (≤ 10 cm height, purple squares). Data labels indicate the number of years since tree death.

Many studies of wood decomposition have incorporated the distinction between snags and fallen boles, but few, to my knowledge, have explicitly considered the effect of CWD height from the ground as a determinant of decay. Some have anecdotally commented on elevated CWD without quantifying any effects. Such was the case for Busse (1994), who conducted a study similar to mine evaluating wood density in insect-killed lodgepole pine snags and CWD in Central Oregon. In spite of lumping suspended and down CWD, Busse observed a remarkably concise distribution of wood density over time since tree fall. However, the first and most notable result Busse reported was the observation that decay class I boles that were elevated off the ground showed no sign of decomposition. Busse (1994) also reported that of 21 decay-class-I boles, 19 were in an elevated position, and all boles in higher decay classes were in contact with the ground. Johnson and Greene (1991) similarly identified 'layers' of CWD which they associated with distinct mortality assemblages (due to fire and self-thinning); bottom layers were from an old fire disturbance assemblage, top layers consisted of the more recent self-thinning assemblage, and middle layers were a combination of the two. The authors did not elaborate to define the physical proximity of these respective layers to the soil surface, but a likely assumption is that the top layers were further from ground and the bottom layers rested on the ground. Despite the description of CWD layers, Johnson and Greene (1991) did not characterize this feature quantitatively or discuss the potential influence the layering may have had on their results.

Shorohova and Kapitsa (2014) characterized decay rates for a variety of dead wood positions, among other factors, and found that leaning logs took longer to decompose than fallen logs. Of the species considered, pine was the most resistant to decay. Van der Wal et al. (2007) found that woody fragments buried in soil to a depth of 3 cm exhibited higher fungal growth than

samples incubated on the soil surface. My findings of accelerated carbon density loss for samples closer to and embedded in the forest floor concur with the results reported by van der Wal et al. (2007) and Shorohova and Kapitsa (2014). I chose 10 cm above the duff as an arbitrary threshold to differentiate suspended and down CWD, but visual inspection of the data after the fact suggests that 20 or 25 cm above the soil may be a more biologically meaningful break point to distinguish these groups (Figure 8). The appearance of a break point at 20 or 25 cm from the forest floor may correspond to microhabitat factors such as average depth of persistent snow cover during non-freezing weather and boundary layer effects of vegetation cover in the study area.

Temporal effects

Time was a stronger predictor of decay in down CWD than it was for suspended CWD. Of the two time factors evaluated, years since fall was a good predictor of carbon density loss in CWD resting within 10 cm of the forest floor, but years since death did not rank highly in any of the candidate models. By contrast, the time since fall was not at all correlated with decay in suspended CWD, and years since death was only a minor predictor of decay (relative to the effect of years since fall for down CWD). These findings for down CWD were consistent with the trends reported by Storaunet and Rolstad (2002) and DeLong et al. (2005), who evaluated the effectiveness of decay classes to estimate time since death and time since fall for *Picea abies* (L.) Karst. (Storaunet and Rolstad 2002), and *Picea glauca* (Moench) Voss x *Picea engelmannii* Parry ex Engelm. and *Abies lasiocarpa* (Hook.) Nutt. (DeLong et al. 2005). Both studies showed that CWD decay classes were more correlated with time since fall than with time since death. DeLong et al. (2005) suggested that the lack of explanatory power between decay class and time

since death was due to the variability in standing time for snags before they fall. This is potentially the case for the suspended boles in my dataset. The fact that decay in suspended CWD was not correlated with time since fall, and was only weakly related to time since death suggests that for this dataset, suspended CWD may be as unlike down CWD as they are unlike snags.

Climatic factors

Relative to sample elevation, the coefficients for climate variables were smaller but important for carbon density loss in suspended and down boles, and each position category was affiliated with different season-specific variables. Suspended CWD exposed to higher summer precipitation were more decayed than their drier counterparts. Carbon densities were lower under wetter and colder summer conditions, and higher under drier and warmer conditions. This was contrary to Johnson and Greene's (1991) speculation that wetter cooler conditions limited the potential for microbial activity, resulting in the slower decomposition that they observed in older stands. Johnson and Greene (1991) attributed the wetter colder conditions to the forest structure of the older stands, which were more dense with limited light penetration through the forest canopy. It is possible that the conditions at my sites were less influenced by forest structure, and that for suspended CWD, moisture was a limiting factor for decay. This would explain the positive relationship with precipitation during the growing season.

Other studies have shown general patterns similar to mine with precipitation and temperature being good predictors of decomposition. Trofymow et al. (2002) found that for the Canadian Intersite Decomposition Experiment, temperature and summer precipitation were among the best explanatory variables for litter decomposition (others being chemical traits of the decomposing

substrates). Weggler et al. (2012) reported that precipitation, temperature and evapotranspiration explained changes in wood density for decay class 1 spruce CWD in Switzerland; precipitation was also an important predictor of wood density in decay classes 2 and 3, but not in decay class 4, which had evapotranspiration alone as the best predictor. Similar to what Weggler et al. (2012) reported for decay class 4, my data for carbon density in down CWD are not clearly correlated with precipitation. Rather, my data show a positive trend with mean winter temperature; e.g., samples exposed to colder winter temperatures were more decayed. The lack of a clear influence of precipitation for down CWD may indicate that, with the closer proximity to the forest floor, the moisture content of CWD – and therefore, the potential for microbial activity – is regulated more by soil moisture than by precipitation. This would support my hypothesis that grounded CWD are subject to up-wicking of soil moisture, easier colonization by soil-borne agents of decay, as well as boundary layer effects of vegetation cover, temperature moderation, and snow cover.

The pattern of higher carbon density at warmer seasonal temperatures for both suspended and down CWD was not expected. It is possible that for suspended boles, warmer summer temperatures facilitate drying of the substrate, and thus suppress the potential for microbial activity. This would correspond with the notion that moisture is a limiting factor for decomposition in MPB-affected forests, and explain why higher temperatures are affiliated with less decay in wood. Boddy (1983b) identified optimal temperature ranges for activity of decomposition fungi, but it is unlikely that the influence of temperature on fungal activity in central BC would be on the right-hand side of such a bell-shaped temperature response curve, especially for winter temperatures in the case of down CWD. One explanation for the apparent trend of decreasing carbon density with decreasing temperatures may have to do with the

combination of temporal and geographic dynamics of the MPB outbreak in BC. The sites associated with the 1980s MPB outbreak are in the southwest portion of the study area, which is also the driest and coldest. Consequently, these sites have the oldest MPB attack, and few sample boles from the same climate regime represent the more recent, less decayed cohort of MPB-killed trees. On the wetter sites in the northeast part of the study area, the majority of MPB-killed trees died more recently as the 1990-2010s outbreak swept northeastward. The effect of this temporal sequence across the geographic area likely explains some of the apparent trend of more advanced decay on colder sites. This was a risk I tried to avoid during field sampling by seeking a temporally diverse array of beetle-killed trees at each site; however, as is often the case in studies of natural ecosystems, conditions are not necessarily conducive to ideal scientific methods.

Snags

The evidence presented here supports the hypothesis that carbon density in MPB-killed snags does not change considerably as long as boles remain upright. The persistence of carbon density in snags was consistent with the findings of similar studies evaluating wood density. For insect-killed snags and live lodgepole pine in central Oregon, wood density was indistinguishable (0.43 ± 0.04 and 0.44 ± 0.03, respectively) (Busse 1994). Lodgepole pine snags that died by non-insect causes (fire or self-thinning) in south-western Alberta also showed the same pattern of stable mass density for up to thirty years after tree death (Johnson and Greene 1991). In my dataset, the range of carbon density in sampled snags was more or less stable for a timespan of approximately thirty years post-mortality (Appendix D, Figure D1).

Although not significantly different, the broader range of snag carbon densities compared to live lodgepole pine suggests that minor degradation and/or changes in wood properties do occur, at least for some snags (Appendix C, Figure C1). The lack of a trend in carbon density over time or with the climate variables considered demonstrates that the capacity for decay in snags is limited, and, that the decay that does occur is unrelated to these parameters. Lewis et al. (2006) found that drying, blue stain, and checking were the main factors affecting wood quality in the first few years following MPB attack, but degradation did not otherwise progress, except at the base of the tree where moisture enabled continued microbial activity. The fact that carbon density of snags does not show a pattern of decline over time confirms that the characteristics of snag wood at 1.3 m height (where I collected samples) are independent of the factors that dictate the likelihood of falling.

Although there is much evidence supporting the hypothesis that lodgepole pine snags can remain more or less sound for extended periods after mortality, it is important to recognize that the individuals that persist are not representative of the whole population. Presumably, other snags that have succumbed to more rapid degradation pathways are no longer standing. Thus, snag fall rates are an integral component factoring into wood decomposition, which I discuss in more detail later on.

Curve-fitting implications

Patterns of DOM decay over time have been described statistically with linear, negative exponential (single or multiple), and sigmoidal (also called negative/reverse sigmoidal, or lag-time) models (Figure 9), as well as logarithmic variations. Of these, the exponential model (Figure 9 B) is the most commonly used for wood (Olson 1963, Harmon et al. 1986), although

evidence suggests that models incorporating a time lag (i.e., negative sigmoidal, Figure 9 C) may represent the full process of decay more accurately (Boyce 1923, Buchanan and Englerth 1940, Means et al. 1992, Busse 1994, Laiho and Prescott 2004).

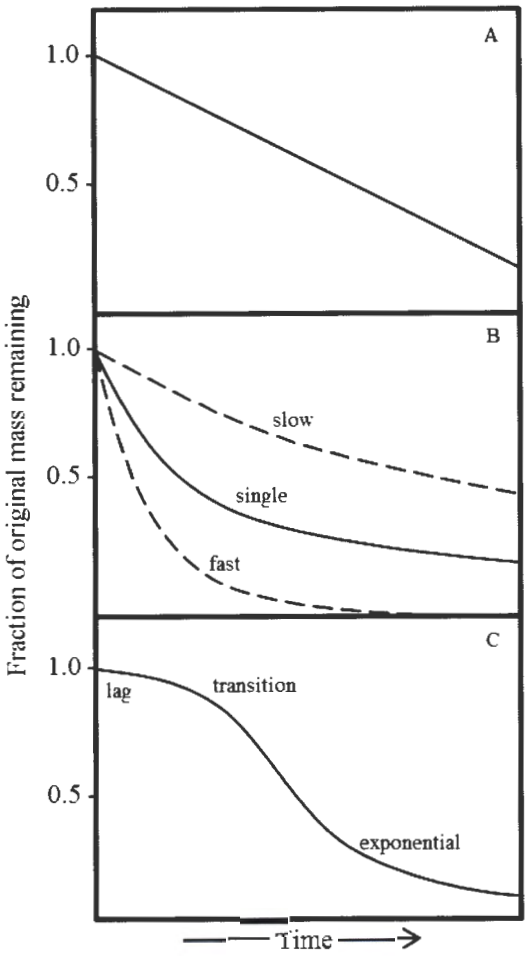


Figure 9. Three models for estimating wood decomposition (e.g., loss of mass or density) over time: the linear model (A) corresponds to a constant rate of decay, regardless of the amount of substrate. Single and multiple exponential models (B; solid and dashed lines, respectively) represent constant rate(s) of decay relative to the amount of substrate available. The lag-time or sigmoidal model (C) incorporates an initial period of minimal decay to reflect the time during which decay agents become established in dead wood; this lag period transitions to an exponential rate as optimal decay conditions evolve. Panels B and C adapted from Harmon et al. (1986).

Despite efforts to compare the fit of different models, many cases appear ambiguous with multiple models fitting a single dataset equally well. Graham and Cromack (1982) applied linear, exponential, and logarithmic models to their chronosequence data for spruce and hemlock decomposition in the Olympic Peninsula (Washington state, USA), and found that all three models fit the data equally well. Similarly, Busse (1994) concluded that a single exponential decay model fit chronosequence data for lodgepole pine in central Oregon very well, and, recognizing the variability of decay rates over time, tested a double-exponential model to accommodate distinctly different DOM components, but this did not improve the fit. In their comparison of a single exponential and a summation-exponential model (equivalent to multiple exponential) for Douglas-fir decomposition in the Western Cascades of Oregon, Means et al. (1985) found no conclusive improvement in fit with one model over the other.

Much of the uncertainty about wood decay rates may be attributed to contrasting interpretations of the evidence of decay patterns over time. Though many studies have reported good fits with the single exponential model, it assumes that the decay rate remains constant through time – an assumption that is too simplistic for scenarios of major forest disturbances (Harmon et al. 2000) and changing climate regimes. Laiho and Prescott (2004) pointed out that many datasets that have been fit with exponential models would actually be better suited to a sigmoidal model, incorporating a time lag before rapid onset of decay.

In contrast to the ambiguity in older literature about best-fitting decay curves, a number of more recent studies decisively indicate that in some species, and in *Pinus* in particular, decomposition follows a sigmoidal decay curve. The vector-based[12] observations made by Harmon et al. (2000)

[12] The vector-method is described in more detail in the Background section.

yielded decay rates differing by an order of magnitude for different periods of decomposition. They also found that the short-term decay rates of the vector method were higher than the overall rates generated by the chronosequence method. By being lower than the vector-produced rates, the chronosequence data suggest that earlier phases of the decomposition process were slower. Harmon et al. (2000) therefore concluded that for *Pinus sylvestris* in northwestern Russia and other species exhibiting similar patterns, the negative exponential model does not accurately represent the variation of decay rates over time. Using a similarly novel approach, Freschet et al. (2012) also found that a sigmoidal curve best described the loss of wood density for *Pinus sylvestris* stems in northern Sweden. Laiho and Prescott (2004) pointed out that Busse's (1994) results for *Pinus contorta* appear better suited to a sigmoidal curve than the exponential curve that was reported.

Although a comparison of different decay curves for the data in this thesis would be pertinent in the context of current wood decomposition literature, it was beyond the scope of my research to explore the subject statistically. Visually, the amount of noise in my data suggests that linear versus exponential or sigmoidal comparisons may be inconclusive (Appendix D, Figure D1a, Figure D2a, and Figure D3a). Conceptually, the rates of density loss for the three position categories may be approximated to a stick-model version of a sigmoidal curve, as suggested by Yatskov et al. (2003) for the different phases of decay. The negligible, slow, and faster rates of density loss for snags, suspended, and down boles, respectively, would correspond to the initial lag, onset, and more rapid phases of decay in the first half of a sigmoidal curve. Boddy (1983a) evaluated linear and exponential models as part of her Ph.D. thesis and found that both models described wood decay data equally well (Boddy, unpublished 1980), as many others have found. Evaluation of different decay curves for this dataset therefore remains a project for future work.

In the meantime, following the rule of parsimony (Burnham and Anderson 2002) holds merit: the simple linear models used here reveal some interesting patterns that warrant further investigation.

For CWD decomposition data to clearly demonstrate the suitability of a sigmoidal (or exponential) curve, sufficient observations must be made within the first 5 years of treefall (Fahey 1983, Freschet et al. 2011), and/or tree death. This early lag period is often associated with limited decomposition as wood becomes colonized by decay fungi and acquires optimal moisture conditions (Laiho and Prescott 2004). Therefore, focusing sampling efforts on the early years following tree death and fall would aid in the determination of a best-fitting curve (Freschet et al. 2012). At the time of sampling, my primary objective was to acquire as broad a range of decay conditions as possible, and the resultant minimum years since tree death in my data are 3, 5, and 7 years for snags, suspended, and down CWD, respectively (Appendix C, Table C2). Hence, the number of observations within the first 5 years of tree death is not large. The addition of samples from early decay phases would likely make curve-fitting a more conclusive proposition for my dataset.

To appreciate the importance of model fitting, consider the application of a simulation model for forest carbon emissions using an exponential decay curve. In a simulation of the first 20 years following a major forest disturbance, the decay process would initiate immediately with a high decay rate, and tail off gradually. By contrast, the same 20-year simulation using a sigmoidal decay curve would initiate with an early phase of low/slow carbon release, followed by a gradual increase before the maximum decay rate would be achieved. The resulting prediction of carbon

emissions for the same 20-year period would be lower for the sigmoidal decay curve, compared to the simulation using an exponential decay curve.

In the case of the CBM-CFS3, predictions of forest carbon emissions are used to determine Canada's carbon budget, which emphasizes the need to use the best possible approximation of reality. Therefore, the importance of curve-fitting is clear in the context of over- or under-estimating carbon fluxes from wood decay over time.

MPB-killed wood density and the CBM-CFS3

Until recently, the CBM-CFS3 used exponential decay curves to simulate the loss of carbon from all DOM in forests of all types and tree species across Canada. The four groups of carbon pools that the CBM uses to categorize DOM include the very fast (foliar litter and fine roots), fast (woody litter, branches, small stem wood, and roots), medium (large stem wood and bark), and slow (humified organic matter) carbon pools (described in Appendix A, Table A1) (Smyth et al. 2010). Although exponential decay equations may adequately represent the very fast and fast carbon pools, they overestimate the initial decomposition phase for the medium pool. With the growing body of evidence supporting sigmoidal decay patterns for CWD (Laiho and Prescott 1999, Harmon et al. 2000, Yatskov et al. 2003, Freschet et al. 2012), it has become clear that exponential decay curves are not appropriate, especially considering that tree stem wood accounts for the bulk of above-ground forest carbon (Johnstone 1970). In light of this evidence, the CBM carbon accounting team initiated the transition to a sigmoidal decay curve for snags and CWD in 2014-2015 (C. Smyth personal communication, 2015). While this potentially represents a substantial refinement of decay parameterization for stem biomass in the medium pool, the opportunity to integrate field-based decay rate observations remains.

Because my evaluation of carbon density loss in MPB-killed lodgepole pine was conducted using linear regression models, the resultant decay rates are not directly comparable to the rates (exponential or sigmoidal) used in the CBM-CFS3. For the CBM simulation of MPB impacts on forest carbon balances (Kurz et al. 2008), the model parameters included an annual turnover rate (i.e., transition from one carbon pool to another) of snag carbon to CWD carbon, in conjunction with an annual release of snag carbon to the atmosphere. To simulate annual decay for fallen CWD, portions of the CWD carbon were transferred to the slow decay pool and released to the atmosphere. In order to relate my carbon density observations to the parameters used in the CBM simulation for MPB, further work is necessary beyond the scope of this thesis. This will involve converting my data to be applicable to biomass metrics for broader spatial applications. An important factor addressed by the CBM but unaccounted for in my study is the transfer of carbon to other more recalcitrant biomass pools, in addition to the assumed fate as CO_2; I discuss this component of decomposition processes later in the thesis.

In earlier iterations of the the CBM, including the simulation for MPB, temperature was the only climatic variable included to moderate decomposition (Kurz et al. 2008). Since then, results from the Canadian Intersite Decomposition Experiment have been used to improve the predictive capacity of the CBM (Smyth et al. 2010, 2011). Specifically, Smyth et al. (2010) reported that inclusion of summer and winter precipitation would reduce the error of model estimates; this moisture influence was further developed as a modifier for water stress effects under dry conditions (Smyth et al. 2011). My observations of the influence of summer precipitation for suspended CWD support the theory that decomposition is limited under low moisture conditions.

Bole positions and fall rates

The distinction between suspended and down CWD has had little recognition in wood decomposition research. However, researchers in other fields of study have distinguished between elevated logs and completely downed logs, and the ecosystem functions associated with these two classes. Elevated CWD affect wildlife habitat value, serving as elevated runways for intermediate-sized mammals (Delong et al 2005), and obstructing mobility of large mammals (particularly ungulates) in cases of extreme blow-down events (Cichowski et al. 2008), for example. Fire scientists and forest managers recognize the importance of classifying different patterns and quantities of fuel loading because of the resultant effects on fire behaviour (Page and Jenkins 2007).

Tree fall rates were outside the scope of this research; however, some observations may shed light on factors associated with fall rates in MPB-killed stands in central BC. For example, the range of carbon densities in snags could help parameterize the extent of potential decay for snags in simulation modelling. The number of years that boles stood prior to falling (as determined for all fallen CWD) may be an indicator of fall rates for these and other MPB-affected forests. Of the 100 suspended and 58 down CWD samples assessed in this study, half had fallen within 13 to 14 years of tree death, and all boles had fallen by 50 to 75 years. (Appendix E, Figure E1). In simple terms this equates to annual fall rates of 3.5 to 3.9 % for the first half of all snags, which are comparable to snag fall rates reported by DeLong et al. (2008) in wet spruce-fir forests not noticeably affected by insect outbreaks. Fall rates in long-term MPB monitoring plots in central BC were in the same range (C. DeLong and B. Rogers (MFLNRO), unpublished). In the current dataset, snags persisting beyond 13 or 14 years fell at slower rates of 0.81 to 1.35 % per year.

The slower fall rates for the persistent snags were consistent with those reported by Lewis and Hartley (2006) for MPB-killed pine in central BC. In contrast, fall rates have been higher (7 % per year) on a nutrient-poor site with small lodgepole pine in east-central BC (D. Seip personal communication, 2015).

Another observation from my dataset suggests that boles falling sooner are more likely to stay suspended, and boles that remain standing longer are more likely to fall directly to the ground (Appendix E, Figure E1). This may indicate physical changes in persistent snags prior to falling, e.g., loss of branches with which they might otherwise become hung up on other trees during fall, or be supported off the ground in the absence of catching other trees on the way down. Trees that remain standing longer may also succumb to extensive heart rot protected by a shell of undecayed sapwood (case-hardening). When these trees *do* fall, they are more likely to break at impact points along the stem and hence result in more ground contact.

The pattern of earlier-falling boles remaining suspended may reflect demographics of the stand and the episodic nature of disturbances in lodgepole pine forests. When mass mortalities occur as in an MPB outbreak, heavy wind events are likely to result in many boles falling at once (i.e., blowdown) into a complex matrix of suspended CWD. Higher stand densities may also correspond to more CWD in a suspended position because of the greater likelihood of falling snags intersecting other boles on the fall trajectory. In contrast, boles that persist longer as snags may be the result of single-mortality events or legacies from earlier outbreak events.

Reflections for future consideration

Metrics of wood decomposition

Many approaches exist for estimating carbon losses from decaying wood, including various forms and combinations of quantifying real-time CO_2 emissions and monitoring changes in wood characteristics over long periods (LIDET 1995, Jomura et al. 2008, Brown et al. 2010). Quantifying the carbon remaining in coarse woody debris (CWD) is one method for estimating carbon losses; however, this approach requires several labour-intensive steps as well as costly elemental analyses (Laiho and Prescott 1999, Preston et al. 2006, 2009). Evaluating changes in the density of dead wood is simpler and less costly, so this approach has been used extensively alone and in conjunction with other parameters as a means of characterizing wood decay (Graham and Cromack 1982, Johnson and Greene 1991, Busse 1994, Paletto and Tosi 2010, Sakai et al. 2012, Fraver et al. 2013). Fewer studies, however, have demonstrated the relationship between wood density and carbon content per unit volume (i.e., carbon density) in decayed wood samples (Sollins et al. 1987). Expressing decay in terms of decayed mass per unit green volume or green mass is an important distinction because it provides a way to compensate for biases introduced by volume and/or mass losses in samples of advanced decay (Holub et al. 2001, Fraver et al. 2013). In particular, carbon concentrations reported in many decomposition studies only reflect the proportion of carbon relative to the concurrent composition of other elemental constituents; these decayed proportions do not necessarily represent the chemical profile of green wood, and may therefore be biased.

Significance of position categories and management implications

My sampling strategy was to sample one snag for every two fallen boles; it can be assumed that the selection of suspended or down CWD was random, based on the availability of CWD in these positions. Of the 155 samples from fallen boles, 99 were suspended and 56 were on the ground. If the proportional representation of suspended to down CWD in my dataset reflects the abundance of CWD in these respective positions on the landscape, then the slower decay rates of suspended CWD should be taken into consideration when determining stand- or landscape-scale carbon emissions from DOM.

The relative abundance and distinct decay patterns of suspended versus down CWD have implications not only for forest carbon fluxes in unmanaged (i.e., not harvested) forests, which were the focus of this thesis, but also for the management of CWD on harvested sites. Timber harvesting is known to render forests net carbon sources for at least 8 years following cutting (Fredeen et al. 2007), due to the removal of living biomass, fragmentation and accelerated decay of residual dead woody material, and increased respiration of disturbed soil organic matter. Therefore, efforts to retain snags and a higher proportion of suspended CWD (relative to down CWD) on harvested sites may reduce the rate at which carbon is released from harvesting disturbances. Encouraging harvesters to incorporate structural CWD complexity into harvesting operations will aid in achieving this objective. Implementation should include avoidance of crushing or fragmenting existing CWD, and leaving or creating suspended logs in and around wildlife tree patches and throughout the cut area. Such a management strategy would enable the carbon-fixing capacity of cut blocks to recover somewhat with the growth of vegetation and planted trees before the progression of carbon release from decomposition gets underway.

This recommendation aligns with existing CWD management guidelines in BC for biodiversity value on harvested sites. Work by Lloyd (2004) pointed to the importance of retaining snags and longer and larger diameter pieces of CWD in elevated and leaning positions during logging activity to improve habitat availability for wildlife, invertebrates, and vegetation whose persistence depends on these structures. As stated in the Forest Practices Code Biodiversity Guidebook, 'the more that managed forests resemble the forests that were established from natural disturbances, the greater the probability that all native species and ecological processes will be maintained' (Parminter 1995). The BC Chief Forester further emphasized that leaving snags, stubs (snags cut off at several metres height), and elevated logs of longer length ($\geq$ 10 m) and larger diameters ($\geq$ 20 cm) on harvested sites will perpetuate diversity of CWD structures over the course of secondary forest development (Snetsinger 2010). The slower decomposition and higher abundance of suspended CWD that I observed in unmanaged forests thus identifies another reason to manage for CWD complexity during salvage or regular harvesting operations. Maintaining an array of CWD positions and age classes throughout the harvesting and regrowth phases of managed landscapes will not only fulfill distinct ecological functions for biodiversity, but will also moderate the release of carbon from wood decomposition.

Permanent sample plots established to monitor the long-term ecological effects of MPB in unharvested forests are a complementary source of data to this thesis and to further specify CWD management objectives. Observations from the Beetle Ecosystem Monitoring project (BEM, C. DeLong and B. Rogers (MFLNRO), unpublished) quantify relative amounts of CWD by position categories, residence times of suspended boles, and snag fall rates, which are important pieces in the bigger picture of wood decay over time. The long-term BEM data together with my thesis data will potentially provide a valuable quantitative basis with which to a) calibrate wood decay

simulations for calculating forest carbon fluxes, and b) refine objectives for CWD management on harvested sites.

Other fates of carbon from decomposing wood

One common assumption in many decomposition studies, and more alarmingly in the context of carbon simulation models, is the notion that all carbon lost from decaying wood is released entirely as CO_2 to the atmosphere. Some authors have pointed out quite importantly that there are alternative fates for the carbon stored in decomposing wood. Holub et al. (2001) and authors cited therein suggest CWD mass losses are likely due to a combination of leaching, physical removal by animals and invertebrates, fungal biomass, vegetation uptake, and fragmentation, in addition to the commonly emphasized heterotrophic respiration. Decayed organic material can make up a substantial and long-lasting portion of the forest floor in coniferous forests, especially on wetter sites or in wetter climates (Sanborn et al. 2011).

Fragmented CWD will decay more quickly than entire logs because of the increase in exposed surface area. Lambert et al. (1980) found that decay rates of fragmented *Abies balsamea* boles were faster than those of unbroken boles. Graham and Cromack (1982) acknowledged that they may have underestimated decay rates by not accounting for fragmentation. I observed multiple stem breakages in a minor portion of my sampled boles, and deliberately avoided sampling within 1 m of these fragmented zones. Hence, my results may underestimate decay rates by the exclusion of fragmented wood in my sample inventory. Alternatively, my results may overestimate decay rates if it is assumed that all carbon losses exited exclusively in the form of CO_2. Relative to other softwood species, pine wood tends to be more resistant to decay, and thus, less susceptible to fragmentation during falling (Angers et al. 2010). Therefore, this

particular degradation pathway is likely to be variable and dependent on many factors, including species-specific wood traits (Weedon et al. 2009).

Moisture content, volume determination, and implications for decay rate estimates

Although wood density is a simple metric for characterizing wood decay, it is influenced by a number of factors that must be accounted for in order to avoid measurement errors, as pointed out by Harmon et al. (2000), Laiho and Prescott (2004), and Williamson and Weimann (2010). Because the volume of wood changes depending on its moisture content (Heygreen and Bowyer 1996), measurements of volume are specific to the moisture content of wood at the time of measurement. Moisture contents should therefore be reported with wood densities for data to be comparable among studies.

In this study, samples were dried at 102 °C as recommended by Williamson and Weimann (2010) after being stored for several months, so the pre-oven weights did not reflect field MCs in most cases. As a means of detecting the field MCs associated with field-based volumes, I compared the percent of moisture lost from freezer-stored samples to that of the air-dried samples. Freezer-stored samples did not change in volume or MC because they were wrapped in plastic, and the water present in the wood was immobilized.

A second factor complicating the use of wood density is the loss of mass and volume occurring with increased decay. As pointed out by Fraver et al. (2013), estimates of wood density for chronosequence studies are prone to be biased if loss of volume is not accounted for in highly decayed samples. Similarly, elemental concentrations of decayed samples do not reflect the overall change relative to undecayed wood, because the original mass has been reduced (Holub

et al. 2001). Solutions to these issues include implementing a 'collapse ratio' to extrapolate green-wood volume from the horizontal diameter of decayed logs (Fraver et al. 2013), or volume-adjusted concentrations, which express elemental concentrations of decayed wood relative to the mass of undecayed wood (Holub et al. 2001). Few of the sample logs in this study were decayed to the point of losing volume through either fragmentation or collapsing. For those that were, the original shape of each log was apparent enough that measurements for green-wood volume were determined with confidence. By using a volume-based concentration of carbon (i.e., carbon density) as the primary indicator of wood decay, the issue of mass loss pointed out by Holub et al. (2001) is avoided.

In retrospect, several methodological factors employed during this research caused undue complexity for other portions of the study; therefore, the following points may be useful considerations for future work:

- Oven drying temperature is an important factor: it should be >100 °C to ensure 100 % of moisture is evaporated, but at the cost of losing some C via volatiles (~2 % of mass) (Williamson and Weimann 2010). Freeze drying is an alternative to prevent loss of volatile C compounds, but this option was limited by the size of the freeze dryer at UNBC, which could not accommodate a full-size cookie, not to mention many of them.
- Field volume is recommended, as was used here; however, field measurements should include the associated weight of samples **in the field** to ensure proper determination of moisture content. Measurement of field volume is also important to avoid the complication of shrinkage from drier storage conditions.

- Wedge samples for snags were not ideal because of the inability to measure volumes in the field, and because of the potential biases introduced by having different proportions of heartwood and sapwood compared to disc samples. I address the potential errors associated with wedges in the next section. In general, to avoid a sequence of complications, a consistent sampling strategy (e.g., cookies) is advisable for all boles.

Sources of error

A weakness of this study was the lack of adequate sample size for the live and standing dead categories. This limitation in the dataset was the result of not being qualified to fall trees in order to collect full disc/cookie samples (the preferred sampling method used for suspended and down logs). Wedge samples from live and dead standing trees were the compromise in order to obtain some limited data from these categories. Potential sources of error due to this compromise include different proportional amounts of heartwood and sapwood compared to cookies, and differences in wood density, extractive content, and susceptibility to decay. Heartwood and sapwood of lodgepole pine do not differ significantly in lignin content (Campbell et al. 1990), so the disproportionate amount of heartwood to sapwood in wedges may not affect density measurements relative to those of full discs based on lignin. However, Koch (1996) reported that chemical composition of lodgepole pine varied by early wood and latewood, as well as by sapwood and heartwood. Extractives, which generally reduce the susceptibility of wood to decay, are found in higher concentrations in heartwood (Harmon et al. 1986). Fungal activity is therefore likely to be quite different, and sapwood may succumb to decay before heartwood. Woo et al. (2005) demonstrated that within 8 months of attack, physical and chemical properties of MPB-killed lodgepole pine heartwood and sapwood were different from

those of green, un-attacked pine wood (although these results were based on samples from a single tree in each category). Wedges from old snags may therefore have lower wood density values than would be found in equivalent disc samples, due to the higher proportion of extractive-poor sapwood in wedges compared to disc-shaped samples.

The effect of bole diameter on decay rates was not included as an explanatory variable in this study (see Appendix C, Table C1 for summary statistics). Many authors include bole diameter as a covariate when evaluating the effects of other predictors (Cornelissen et al. 2012), and many studies identify diameter as an influential factor in wood decomposition. The decision to not include diameter was based on two factors. First, my preliminary diagnostic evaluation of the data suggested that a relationship did not exist between carbon density and sample diameter; an observation that has been common (Harmon et al. 1986). Secondly, during the process of constructing candidate models for AIC_c evaluation, it was important to limit the predictor variables to a maximum of five per model in order to not exceed the allowable degrees of freedom relative to the number of observations. It was also important to keep the number of candidate models for each position category below twenty, as recommended by Burnham and Anderson (2002). Given these circumstances, I chose to exclude sample diameter as a covariate.

My rationale for taking two samples from fallen boles was to capture the within-bole heterogeneity of decay, and indeed, the extent of decay within individual logs spanned the extremes from completely sound wood to advanced decay (Appendix E, Figure E2). Hence, the wood densities of all samples plotted together over time had a much broader range of variability than observed by Busse (1994). Another factor that may partially explain the range of wood densities in my dataset is the inadvertent inclusion of branch nodes, scars, or reaction wood in

CWD cookies. Johnson and Greene (1991) pointed out that these features will skew density measurements, presumably in the higher direction. I generally tried to avoid sampling wood that was not clear-grained, knowing it may lead to the overestimation of sound wood, but I was also conscious that to entirely exclude these features could potentially skew the dataset to lower carbon densities. In the interest of representing the overall population, therefore, I did not rigorously exclude wood with branch nodes or abnormal growth if it happened to occur at an otherwise suitable sampling point along the bole.

CONCLUSIONS

Of all the aboveground biomass in forested ecosystems, tree boles constitute the largest reservoir of forest carbon. Net forest carbon balances rest heavily on the relative amounts of living and dead bole wood, and the demographic distribution of deadwood across all stages of decay. The outbreak of MPB in central BC and the prediction of large carbon emissions from affected forests highlight a lack of knowledge about regionally-specific wood decay rates. This knowledge gap was the motivation for this project.

The objective of my research was to quantify the rate of carbon density loss from decaying MPB-killed lodgepole pine bole wood, and characterize the decay process in terms of basic physical and climatic attributes. In order to use carbon density as the primary metric of wood decay, I first validated the assumption that carbon density can be readily determined from wood density. Wood density was a very good predictor of carbon density ($r^2 = 1.00$); this relationship was further verified by an observed low variability in carbon concentration across the range of a 76 % reduction in wood density.

The evidence presented here strongly suggests that standing, suspended, and down boles are differentiated by rates of decay, as well as by differences in the importance and magnitude of seasonal climate variables. These observations supported my first three hypotheses of limited decomposition in snags, and progressively faster decay in suspended and down CWD. Bole height off the ground was the single best predictor of carbon density for both suspended and down CWD. Excluding the influence of other predictors, carbon density declined four times faster with proximity to the soil in down CWD than it did for suspended CWD. Elevation of CWD from the ground has not been acknowledged or quantified in most wood decay literature, but the importance of this factor in the current dataset suggests that it is a key indicator of decomposition processes, and should be considered in future work.

The pattern of lower carbon densities with increasing summer precipitation for suspended CWD was consistent with the expectation of my fourth hypothesis. A rather surprising outcome counter to my expectation was a positive influence of summer temperature on carbon density in suspended CWD, which may correspond to a drying effect under warmer summer conditions, thus limiting the capacity for microbial activity. The correlation of carbon density and climate variables affirms recent research that also identified seasonal precipitation as a valuable predictor of decay (Smyth et al. 2010).

Completely downed CWD lost carbon density more rapidly than suspended CWD, and this loss was affiliated with years since fall. Years since death and summer climate variables were completely excluded as useful explanatory variables for down CWD. Winter temperature had a greater effect on carbon density than did precipitation, and this relationship was positive, as summer temperature was for suspended CWD. This was counter to my expectation of more

decay with warmer temperatures. For down CWD, the demographic distribution across the study area is mostly older CWD at colder sites, and mostly younger CWD at warmer sites, which could produce the same trend. Because of the confounded nature of these data, drawing conclusions of biological significance would be tenuous.

Carbon density in snags did not correlate well with any of the predictor variables considered, which suggests that as long as boles remain upright, they are largely unaffected by climate variability. This was consistent with what others have found (Johnson and Greene 1991), and suggests that the factors influencing bole survival are largely related to decay at the base of the tree, but not higher in the bole (Mitchel and Preisler 1998).

This thesis contributes a small but important piece of knowledge toward a better understanding of the broader forest carbon flux picture. The future work of integrating these observations into the decay component of the CBM-CFS3 and other forest carbon models is expected to improve the accuracy of model predictions of forest carbon fluxes following insect outbreaks such as the MPB. The accuracy of forest carbon flux predictions is vital for implementing the best possible management of forests, not only for resource value but also for ecosystem integrity and resilience.

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APPENDIX A. CARBON POOLS OF THE CBM-CFS3

Table A1. Carbon pools of the CBM-CFS3*

CBM-CFS3 pool	Description
Merchantable + bark (SW or HW)	Live stemwood of merchantable size plus bark
Other wood + bark (SW or HW)	Live branches, stumps and small trees including bark
Foliage (SW or HW)	Live foliage
Fine roots (SW or HW)	Live roots, approximately < 5mm diameter
Coarse roots (SW or HW)	Live roots, approximately ≥ 5mm diameter
Snag stems DOM (SW or HW)	Dead standing stemwood of merchantable size including bark
Snag branches DOM (SW or HW)	Dead branches, stumps and small trees including bark
Medium DOM	Coarse woody debris on the ground
Aboveground fast DOM	Fine and small woody debris plus dead coarse roots in the forest floor, approximately ≥ 5 and < 75mm diameter
Aboveground very fast DOM	The L horizon comprised of foliar litter plus dead fine roots, approximately <5mm diameter
Aboveground slow DOM	F, H and O horizons
Belowground fast DOM	Dead coarse roots in the mineral soil, approximately ≥5 diameter
Belowground very fast DOM	Dead fine roots in the mineral soil, approximately <5mm diameter
Belowground slow DOM	Humified organic matter in the mineral soil

*From Kurz et al. 2009

APPENDIX B. PARAMETER DESCRIPTIONS

Table B1. Field and laboratory parameters: units and definitions.

Variable	units	definition
Site-specific field parameters		
BGCunit		Biogeoclimatic unit
MAT	°C	mean annual temperature
MAP	mm	mean annual precipitation
PPTwt	mm	mean winter precipitation
SiteElev	m	site elevation
Fieldcrew		crew initials
SiteNotes		notes related to site description
Date		date of sample collection
SiteID		site name
Bole-specific field parameters:		
BoleID		tree label
sampleID		sample label
Position		S=standing, DE=down but elevated, DG=down on ground
Angle	degrees	if Position=DE, angle of bole relative to ground surface from tree base: (+) if slope is upward toward tip, (-) if slope is downward toward tip
DBH	cm	diameter at breast height (1.3 m from tree base)
DBH at	m	distance from tree base for DBH if not possible at 1.3 m
Bbark	%	estimated percentage of bark cover on whole bole
Falltype		RP = root plate, RS = root snap/stub, WS = wind snap
WSheight	m	if Falltype = WS, distance from base of tree to snap height (measured at tree pith)
Orientation	degrees	if Positon = DG or DE, compass azimuth from base to tip
Breaks		number of breaks in bole, including WS; breaks above 7.5 cm diameter not counted
Break1…	m	distance from tree base to first break (measured at tree pith); same for second break (Break2), Break3, etc.
BolePhoto		photos of stump, any rot fungi on bole, and down the length of the bole
Branch		branch order applying to most recent living crown (5=needles on, 4=needles off, fine branches present, 3=tertiary branch divisions present, 2=secondary branch divisions present, 1=only primary branches present, 0(?)=no branches present)
Checking		minor = cracks < 2mm wide, major = cracks ≥ 2mm wide, or yes/no for presence/absence
ElevMax	cm	greatest height from forest floor along entire bole
TreeNotes		comments pertaining to entire bole

Table B1 continued.

Variable	units	definition
Sample-specific field and laboratory parameters:		
sampletype		C = Cookie, W = wedge
frombase	m	distance from base of tree at which sample was collected
seglength	m	intact length of bole segment from which sample was collected (if breaks are present in stem), no samples collected above 7.5 cm diameter
cover		canopy cover at sample point: DC = dark conifer (Sw), LC = light conifer (Pl), DD = dark deciduous (Alder), LD = light deciduous (At, Ep), Open = no direct canopy cover (sample point in a gap), and combinations…
samplephoto		straight-up photo above sample point: canopy cover above sample
veg	%	log surface (top-down view) covered by vegetation at sample point
vegSp		vegetation species covering log at sample point (7-letter species codes, etc.)
bark	%	percentage of bark present around perimeter of cookie (before cutting)
Elev	cm	distance from organic soil surface to bottom of log; (+) or (–) for elevated or embedded logs
DecayClass		decay class according to DeLong et al.: 1-5, similar to Maser's
thick	cm	thickness of sample cookie, averaged around circumference of disk
Diam1	cm	diameter of cookie across largest cross-section (or smallest); bold font indicates lab-verified measurement
Diam2	cm	diameter of cookie across smallest cross-section (or largest); bold font indicates lab-verified measurement
Density	g/cm^3	wood density (specific gravity)
YrsDead	years	years from tree death to time of sampling
YrsDown	years	years from tree fall to time of sampling
HeartRot	%	estimated heartwood rot (based on discolouration, not hardness)
SapRot	%	estimated sapwood rot(based on discolouration, not hardness or bluestain)

Date	Site ID	elev (m)	sketch	Field crew	
Subzone/SS	old or new	layout		weather	
	GPS waypt name	dimensions		Photo no.	Description
page	notes				

Bole ID		Scar ID	S/DG/DE ±	° orient	°	photos	check				Laura's ID:
DBH	Sp	# breaks	RP/RS/WS@	bark	%		br. 5-4-3-2-1	bole descr: 0 -			
sample ID		cover	photo	veg	%	± elev(cm)	decay class	thickness	diam ht/wd	rot: H - Ins/B/W	
C/W/co	from base(m)		seg length	bark	%		1-2-3-4-5			S - Ins/B/W/blue	
sample ID		cover	photo	veg	%	± elev(cm)	decay class	thickness	diam ht/wd	rot: H - Ins/B/W	
C/W/co	from base(m)		seg length	bark	%		1-2-3-4-5			S - Ins/B/W/blue	
Bole ID		Scar ID	S/DG/DE ±	° orient	°	photos	checking				Laura's ID:
DBH	Sp	# breaks	RP/RS/WS@	bark	%		br. 5-4-3-2-1	bole descr: 0 -			
sample ID		cover	photo	veg	%	± elev(cm)	decay class	thickness	diam ht/wd	rot: H - Ins/B/W	
C/W/co	from base(m)		seg length	bark	%		1-2-3-4-5			S - Ins/B/W/blue	
sample ID		cover	photo	veg	%	± elev(cm)	decay class	thickness	diam ht/wd	rot: H - Ins/B/W	
C/W/co	from base(m)		seg length	bark	%		1-2-3-4-5			S - Ins/B/W/blue	
Bole ID		Scar ID	S/DG/DE ±	° orient	°	photos	checking				Laura's ID:
DBH	Sp	# breaks	RP/RS/WS@	bark	%		br. 5-4-3-2-1	bole descr: 0 -			
sample ID		cover	photo	veg	%	± elev(cm)	decay class	thickness	diam ht/wd	rot: H - Ins/B/W	
C/W/co	from base(m)		seg length	bark	%		1-2-3-4-5			S - Ins/B/W/blue	
sample ID		cover	photo	veg	%	± elev(cm)	decay class	thickness	diam ht/wd	rot: H - Ins/B/W	
C/W/co	from base(m)		seg length	bark	%		1-2-3-4-5			S - Ins/B/W/blue	
Bole ID		Scar ID	S/DG/DE ±	° orient	°	photos	checking				Laura's ID:
DBH	Sp	# breaks	RP/RS/WS@	bark	%		br. 5-4-3-2-1	bole descr: 0 -			
sample ID		cover	photo	veg	%	± elev(cm)	decay class	thickness	diam ht/wd	rot: H - Ins/B/W	
C/W/co	from base(m)		seg length	bark	%		1-2-3-4-5			S - Ins/B/W/blue	
sample ID		cover	photo	veg	%	± elev(cm)	decay class	thickness	diam ht/wd	rot: H - Ins/B/W	
C/W/co	from base(m)		seg length	bark	%		1-2-3-4-5			S - Ins/B/W/blue	

Figure B1. Field data sheet.

APPENDIX C. DATA SUMMARIES

Table C1. Summary statistics for wood density, carbon density and carbon concentration. Sample size (n), mean (± st. dev.) and range (minimum and maximum values).

Category	Basic wood density* ($g \cdot cm^{-3}$)	C density† ($g\ C \cdot cm^{-3}$)	C concentration ($g\ C \cdot g^{-1}$ wood)
	(n = 10)	(n = 10)	(n = 6)
Live	**0.485** (± 0.023)	**0.247** (± 0.014)	**0.509** (± 0.007)
	0.450 – 0.518	0.228 – 0.267	0.500 – 0.521
	(n = 49)	(n = 49)	(n = 8)
Snags	**0.441** (± 0.045)	**0.224** (± 0.023)	**0.508** (± 0.006)
	0.298 – 0.551	0.153 – 0.279	0.501 – 0.516
	(n = 113)	(n = 113)	(n = 17)
Suspended	**0.385** (± 0.060)	**0.196** (± 0.030)	**0.509** (± 0.005)
	0.237 – 0.545	0.123 – 0.277	0.502 – 0.524
	(n = 68)	(n = 68)	(n = 16)
Down	**0.314** (± 0.110)	**0.161** (± 0.055)	**0.519** (± 0.011)
	0.032 – 0.472	0.020 – 0.240	0.504 – 0.541
	(n = 240)	(n = 240)	(n = 47)
All	**0.380** (± 0.089)	**0.194** (± 0.045)	**0.512** (± 0.009)
	0.032 – 0.551	0.020 – 0.279	0.500 – 0.541

*Wood densities reported represent the full dataset, including the subset analyzed for carbon concentration.
†Carbon densities reported include the samples analyzed for carbon concentration, as well as the remainder of the samples whose carbon densities were derived from the outcome of the preliminary analysis.

Table C2. Summary data for all predictor variables considered for AIC_c models. Data shown are sample size (n), mean (±sd), minimum and maximum. Not all predictors considered were included in AIC_c candidate models.

Categ.	years dead	years standing	years down	sample elevation (cm)	sample diameter* (cm)	MAP (mm)	MAT (°C)	winter precip. (mm)	winter temp. (°C)	summer precip. (mm)	summer temp. (°C)
	.	.	.	.	(n = 4)	(n = 10)	(n = 10)	(n = 10)	(n = 10)	(n = 10)	(n = 10)
Live*	.	.	.	.	17.7 (± 1.5)	575 (± 143)	2.4 (± 0.8)	149 (± 47)	-8.2 (± 0.6)	98 (± 29)	12.4 (± 1.1)
	.	.	.	.	16.2 – 19.1	330 – 814	1.7 – 3.8	73 – 228	-8.8 – -7.3	62 – 148	11.1 – 14.3
	(n = 43)	.	.	.	(n = 49)	(n = 49)	(n = 49)	(n = 49)	(n = 49)	(n = 49)	(n = 49)
Snags*	13 (± 13)	.	.	.	22.6 (± 9)	586 (± 174)	2.7 (± 0.6)	141 (± 61)	-7.3 (± 0.5)	108 (± 34)	12.6 (± 0.9)
	3 – 65	.	.	.	10.8 – 47.7	330 – 914	1.7 – 3.8	65 – 262	-8.7 – -6.4	62 – 177	11.1 – 14.3
	(n = 103)	(n = 100)	(n = 107)	(n = 113)	(n = 112)	(n = 113)	(n = 113)	(n = 113)	(n = 113)	(n = 113)	(n = 113)
Susp.	24 (± 16)	16 (± 13)	8 (± 8)	35 (± 26)	16.4 (± 6.1)	596 (± 181)	2.7 (± 0.6)	148 (± 65)	-7.4 (± 0.5)	108 (± 34)	12.6 (± 1)
	5 – 69	0 – 65	0 – 32	11 – 190	7.3 – 32.8	333 – 914	1.6 – 3.8	65 – 268	-8.4 – -6.4	65 – 177	11 – 14.3
	(n = 67)	(n = 58)	(n = 59)	(n = 66)	(n = 67)	(n = 68)	(n = 68)	(n = 68)	(n = 68)	(n = 68)	(n = 68)
Down	32 (± 23)	20 (± 20)	11 (± 9)	0 (± 6)	18.5 (± 8.6)	555 (± 176)	2.8 (± 0.6)	134 (± 60)	-7.5 (± 0.6)	99 (± 34)	12.8 (± 0.9)
	7 – 87	0 – 73	0 – 32	-19 – 10	8.4 – 48.9	329 – 914	1.6 – 4	67 – 262	-8.9 – -6.4	61 – 177	11 – 14.5
	(n = 223)	(n = 159)	(n = 167)	(n = 180)	(n = 180)	(n = 240)	(n = 240)	(n = 240)	(n = 240)	(n = 240)	(n = 240)
All	23 (± 19)	17 (± 16)	9 (± 8)	23 (± 30)	17.1 (± 7.2)	582 (± 177)	2.7 (± 0.6)	143 (± 62)	-7.4 (± 0.6)	105 (± 34)	12.7 (± 0.9)
	3 – 87	0 – 73	0 – 32	-19 – 200	7.3 – 48.9	329 – 914	1.6 – 4	65 – 268	-8.9 – -6.4	61 – 177	11 – 14.5

*For live trees and snags, data shown for sample diameter are the measured diameters at breast height (DBH).

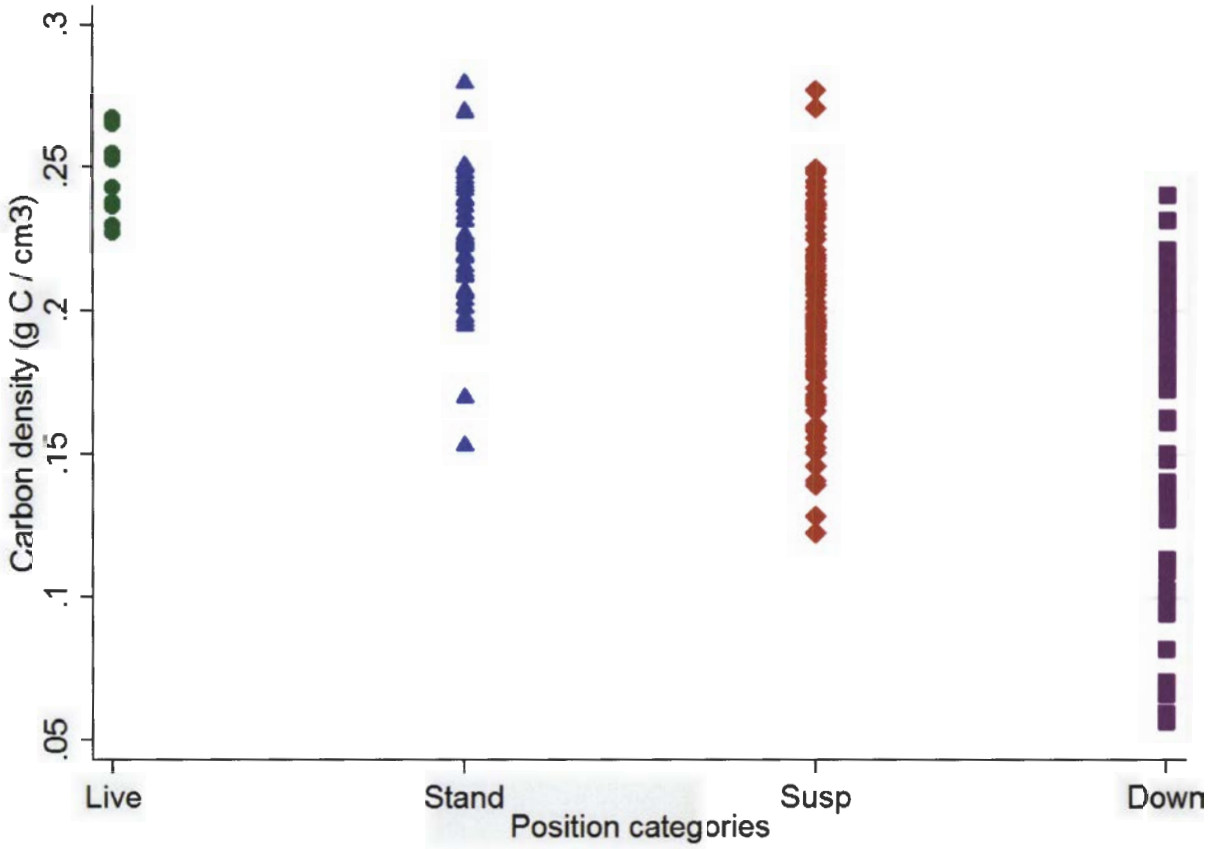

Figure C1. Distribution of carbon density (g C cm^{-3}) in wood samples classified by categories of live lodgepole pine, and MPB-killed lodgepole pine snags (Stand), suspended (Susp), and down CWD.

APPENDIX D. CARBON DENSITY AND PREDICTOR RELATIONSHIPS

Table D1. Regression coefficients for best linear mixed model for carbon density in MPB-killed lodgepole pine snags. Carbon density did not vary appreciably with any of the predictor variables considered, therefore, parameter relationships were not evident in any of the candidate models and the null model was best-ranked.

Model #1 *(null model)*	Coeff.	St. Err.	95 % C. I.
fixed effects			
(intercept)	0.224	0.00352	0.217 – 0.231
Random effects			
Site	4.64×10^{-08}	3.72×10^{-07}	7.11×10^{-15} – 0.0303
st. dev. (residual)	0.0231	0.00249	0.0187 – 0.0285

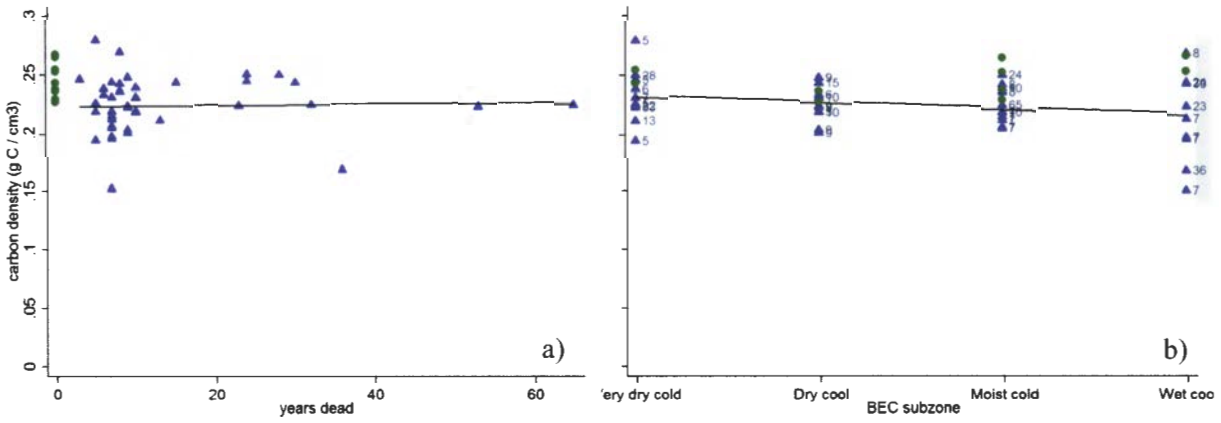

Figure D1. Carbon density (g C cm^{-3}) of snags (blue triangles) and live lodgepole pine (green circles) for reference, versus predictor variables as follows: a) years dead and b) BEC subzones. Data labels indicate the years dead for each snag. Continued on next page.

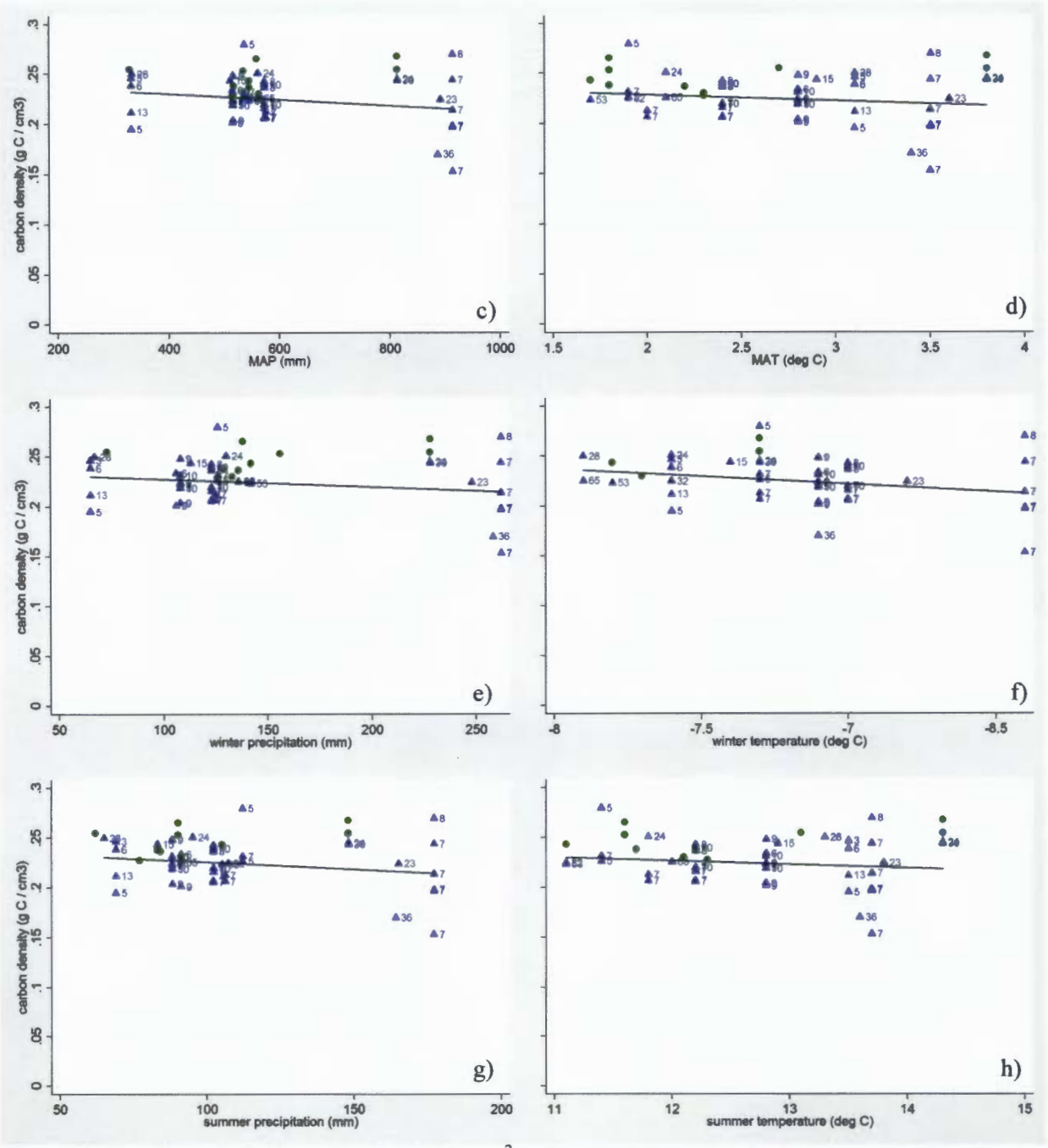

Figure D1 continued: Carbon density (g C cm^{-3}) of snags (blue triangles) and live lodgepole pine (green circles) for reference, versus predictor variables as follows: c) MAP, d) MAT, e) mean winter precipitation, f) mean winter temperature, g) mean summer precipitation, and h) mean summer temperature. Data labels indicate the years dead for each snag.

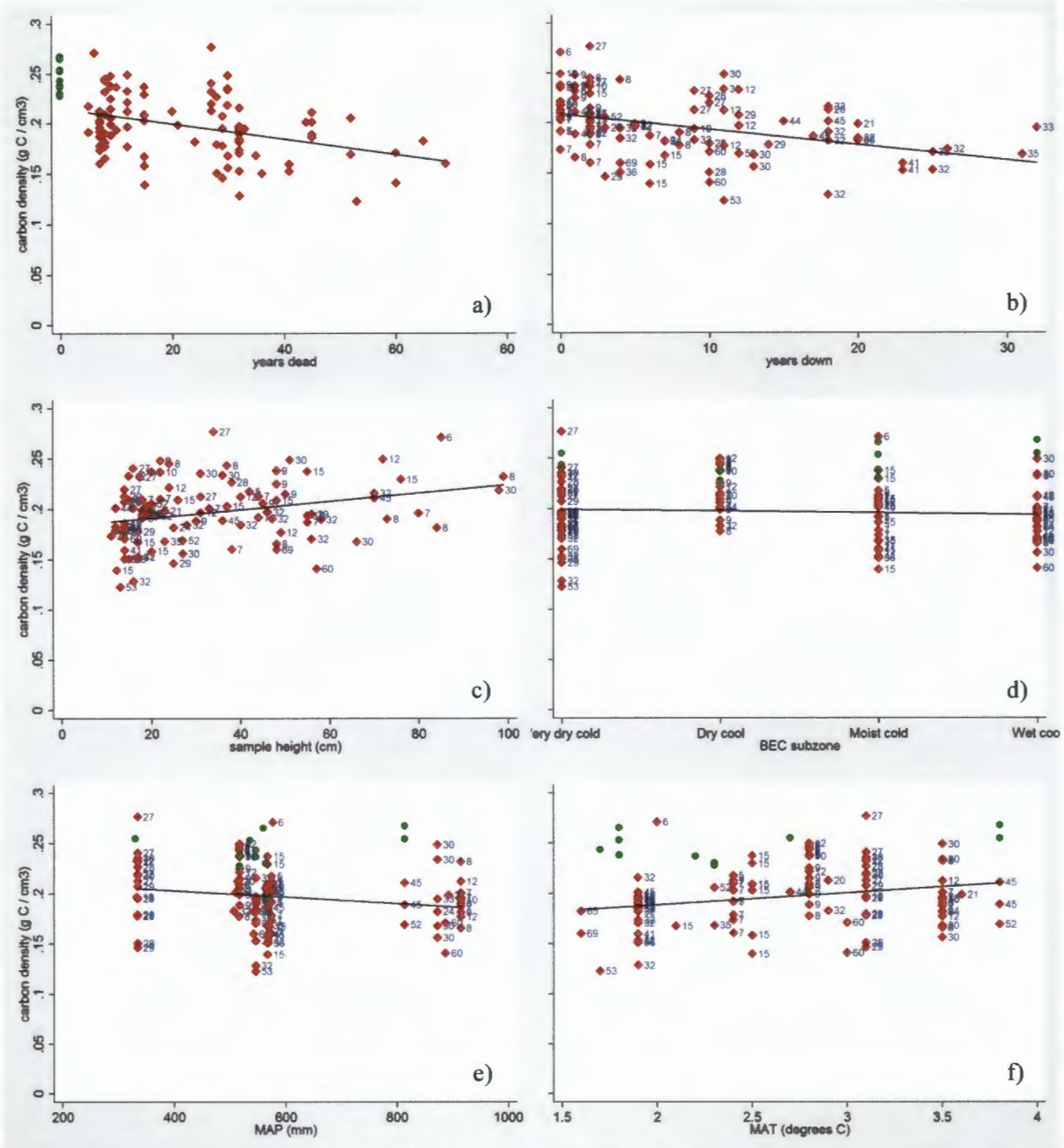

Figure D2. Carbon density (g C cm^{-3}) of suspended CWD (red diamonds) and live lodgepole pine (green circles) for reference, versus predictor variables as follows: a) years dead, b) years down, c) sample height off the ground, d) BEC subzones, e) MAP, and f) MAT. Data labels indicate the years dead for the bole. Continued on next page.

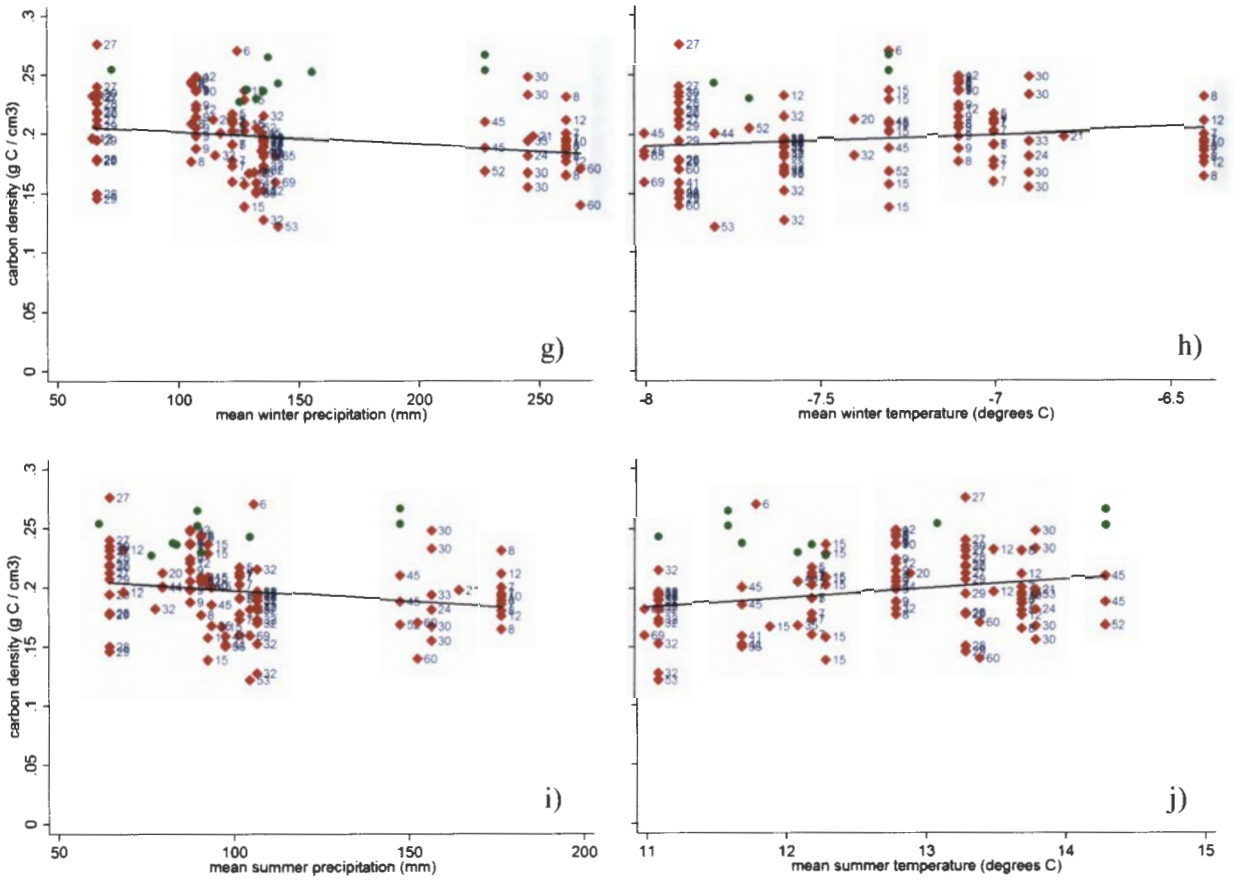

Figure D2 continued: Carbon density (g C cm^{-3}) of suspended CWD (red diamonds) and live lodgepole pine (green circles) for reference, versus predictor variables as follows: g) mean winter precipitation, and h) mean winter temperature, i) mean summer precipitation, and j) mean summer temperature. Data labels indicate the years dead for the bole.

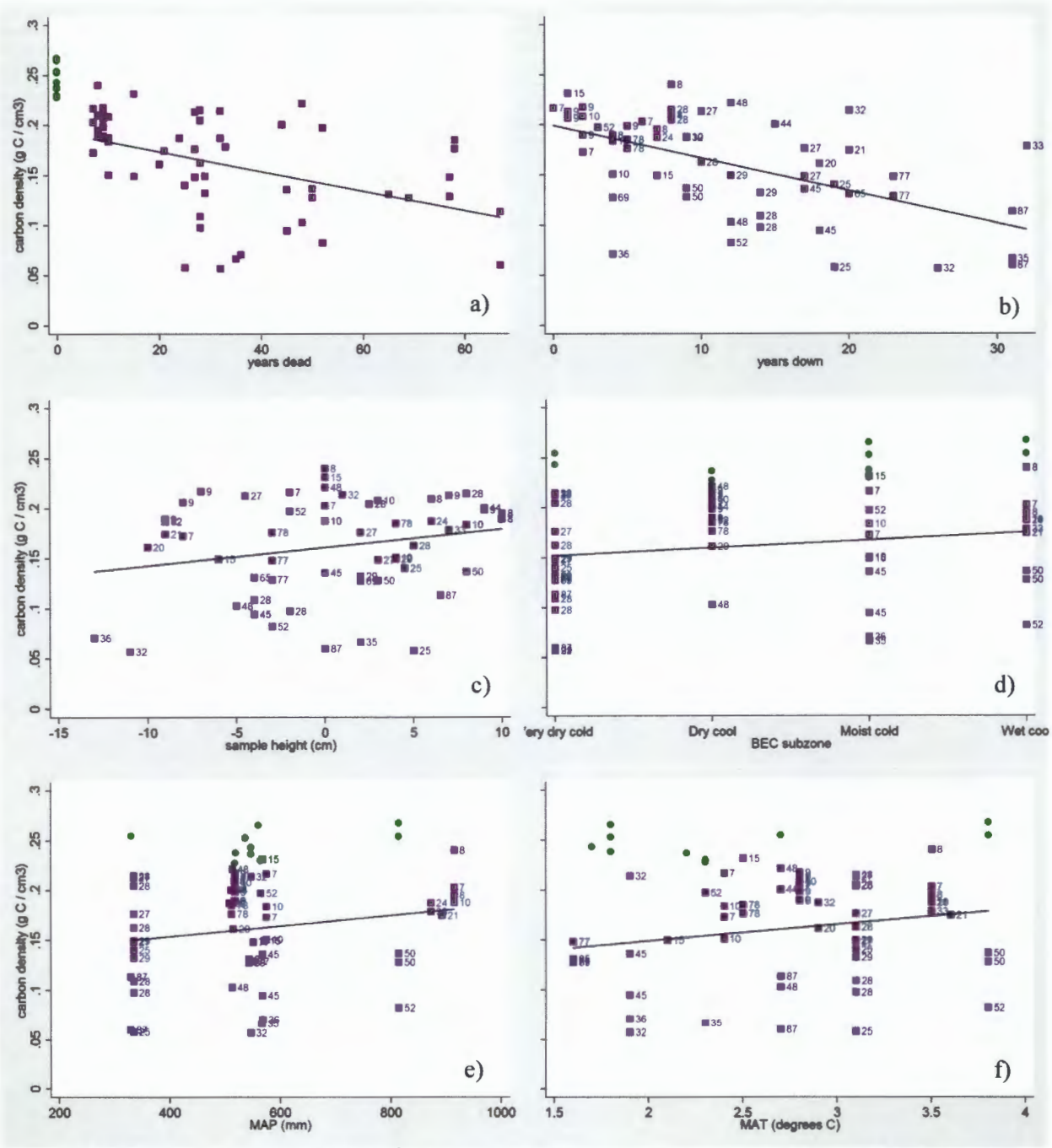

Figure D3. Carbon density (g C cm^{-3}) of down CWD (purple squares) and live lodgepole pine (green circles) for reference, versus predictor variables as follows: a) years dead, b) years down, c) sample height off the ground, d) BEC subzones, e) MAP, and f) MAT. Data labels indicate the years dead for the bole. Continued on next page.

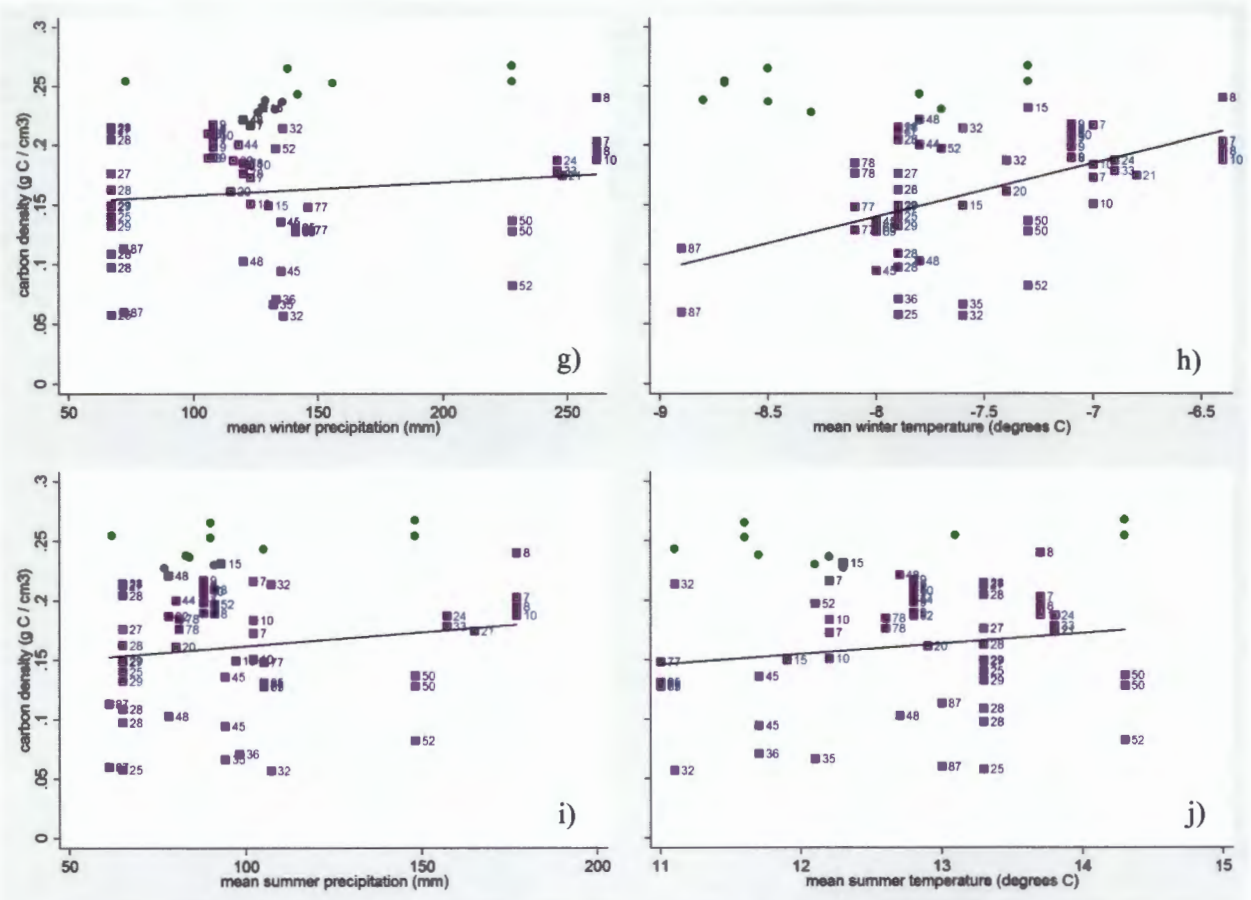

Figure D3 continued: Carbon density (g C cm^{-3}) of down CWD (purple squares) and live lodgepole pine (green circles) for reference, versus predictor variables as follows: g) mean winter precipitation, and h) mean winter temperature, i) mean summer precipitation, and j) mean summer temperature. Data labels indicate the years dead for the bole.

APPENDIX E. TREE FALL-TIMES AND WITHIN-BOLE HETEROGENEITY

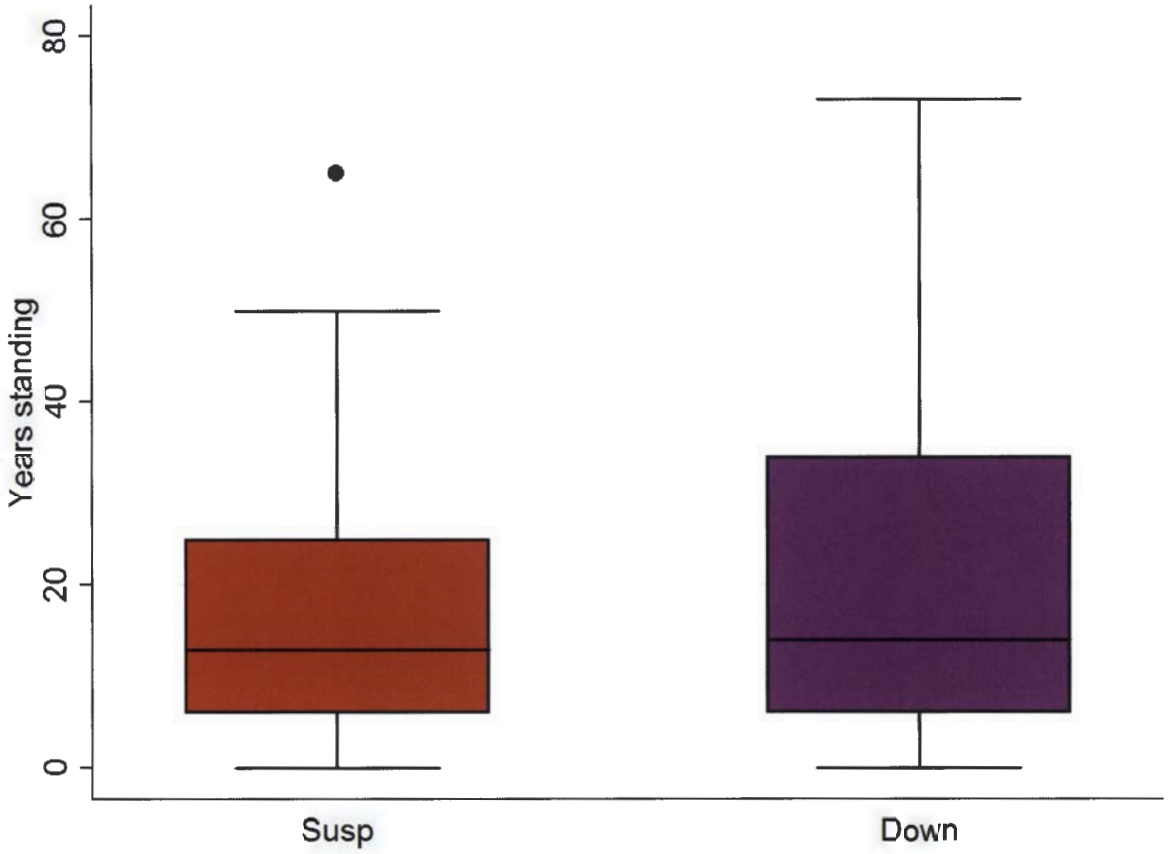

Figure E1. Median and quartiles of the years from tree death to tree fall for suspended (Susp) and Down CWD.

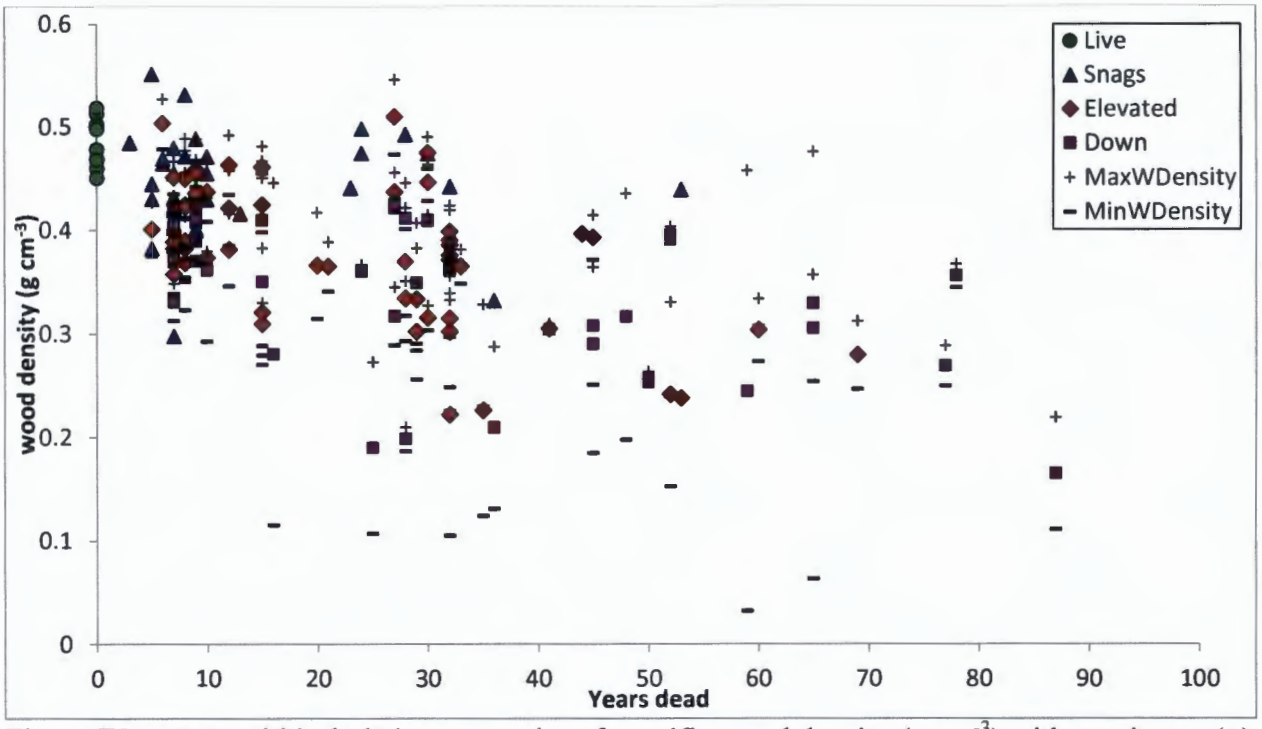

Figure E2. Mean within-bole heterogeneity of specific wood density (g cm^{-3}) with maximum (+) and minimum (-) for each suspended and down bole. Down boles exhibited the greatest variability as demonstrated by the two lowest wood density observations near 60 years dead, which are from boles that also have maximum wood density observations within the range of live trees. Live trees and snags are included for reference only.